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The Northern Bob-White's winter territory

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The Northern Bob-White's Winter Territory

By Paul L. Errington and F. N. Hamerstrom, Jr.

AGRICULTURAL EXPERIMENT STATION
IOWA STATE COLLEGE OF AGRICULTURE
AND MECHANIC ARTS
R. E. Buchanan, Director

ENTOMOLOGY AND ECONOMIC ZOOLOGY SECTION

AMES, IOWA
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FOREWORD

This bulletin is presented for whatever utility it may have from the standpoint of conservation and wildlife management. The institutions and persons cooperating and financing the concurrent Wisconsin and Iowa researches on bobwhites have been strongly motivated by the hope that the findings may have substantial practical application as well as value to pure science.

I. The Wisconsin Quail Investigation from 1929 to 1932 was established at the University of Wisconsin by the Sporting Arms and Ammunition Manufacturers' Institute and the U. S. Biological Survey; the Iowa wildlife research program, 1932 to 1935, at Iowa State College, by the College and the Iowa Fish and Game Commission, cooperatively, with J. N. ("Ding") Darling financially contributing.
The Northern Bob-White’s Winter Territory

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PART I. INTRODUCTORY REMARKS AND TECHNIQUE

This bulletin attempts to bring up to date our knowledge of individual covey ranges or wintering territories of the bob-white quail [Colinus virginianus virginianus (Linn.)] (Fig. 1.)

It is based upon all of the pertinent and reliable data upon the subject at hand, of whatever origin and whatever degree of previous publication. Pertinence and reliability constitute the sole criteria by which we have attempted to judge the eligibility of data used, whether the data support our principal conclusions or not.

While based chiefly upon Iowa and Wisconsin studies, and intended particularly as an aid to bob-white management in those two states, this technical presentation is not confined in its scope by state lines. Very conceivably, the conclusions arrived at may apply to the North-central States region as a whole, or roughly to the northwest portion of the bob-white’s

2. Project 329 of the Iowa Agricultural Experiment Station.

3. Management of a wild species usually means the encouragement of the species under conditions as nearly natural as possible; it lays emphasis upon environmental control rather than legal protection or artificial propagation.

Fig. 1. Bob-white covey feeding. Courtesy of Milton F. Hulburt.
natural and naturally extended geographic range.

Management of wintering territory, under conditions repre­
sentative of the North-central States, is a large part of a com­ple­
plete program of management for the bob-white. It is true that
the direct toll taken by man, as in connection with hunting,
needs a certain amount of regulation, and it may be that greater
management emphasis needs to be placed upon the maintenance
or improvement of nesting conditions. Management may at
times be forced to cope with novel, though drastic, emergencies.
For all of the latter, however, winter in the northern part of the
bob-white’s range seems to be the one supremely critical period
in the life equation of the species, and winter survival cannot
exceed ability of environment to accommodate population.

Winter is a period of increased crisis to bob-white, con­spicu­usly because of emergencies associated with cold and
snow. Less spectacular, is the distinct change in habitability
of the environment for bob-white which is coincident with the
annual transition from autumn to winter conditions of vege­ta­tion.

With the advent of winter, a bob-white population adjust­ment
is typically necessary, even though there be no snow. The
adjustment or “fall shuffle” [Leopold (46) pp., 49-51] takes
place in response to the wholesale seasonal shrinkage of quail­
habitable environment brought about by the withering of
herbaceous vegetation and the loss of leaves of deciduous woods
and brush. It is unquestionably influenced also by changes in
the food supply, occurring naturally or through the agency of
man.

Prior to these regular autumnal changes in bob-white en­
vironment, a given tract of land has a capacity to accommodate
a much greater number of birds. In summer, food is usually
abundant and well distributed, concealment cover may be found
in greater or less quantity nearly everywhere, and the habita­
bility of the land for quail is doubtless high enough to take care
of the adult population plus substantial increases of young.

Then, as winter comes, the bob-white population may find
itself in an environment which has out-shrunk it. Consider­able
acreages of formerly attractive habitat may now be plowed
ground. Other lands, though unplowed, may have plant
growths trampled and pastured flat, or may be swept clean by
burning. Even when unmolested by man, many heavy brush
and weed patches, formerly offering quail cover almost impene­trable to attacking enemies, may stand frost-stripped and open.

By late fall, the total plant growth capable of serving as
effective escape cover may be confined to a few gullies or wood­
lots or watercourses, or to a few other places where vegetation
may be sufficiently dense to give the birds something to get into
in case of danger. Brush heaps, abandoned farm machinery, piles of discarded woven wire, and the like, sometimes constitute the bulk of the utilizable escape cover on some properties.

In brief, not a great part of any area has the quail cover on it by winter that it had in early fall. The net habitability of the residual escape and concealment cover is frequently further lowered by partial or total lack of access to a suitable food supply. The winter environment may be so barren as to be quite uninhabitable. The relation of food and cover to each other is of primary significance in determining the adequacy of bobwhite environment.

We may readily perceive, therefore, how winter environments at their best may be inadequate to accommodate populations existing in comparative security under the more favorable conditions of late summer and early fall. The carrying capacity of an area for bob-white may conceivably be reduced by half or possibly more, simply by the natural seasonal loss of leaves from deciduous vegetation.

The acceleration of bob-white losses from predation commonly noted in late fall is apparently but a manifestation of increased exposure to enemies [Errington (26)], as it corresponds well with cover shrinkage and the incidence of early snowfall. Counts made in the 1933-1934 field studies in southern Iowa [Errington and Hamerstrom (35)] indicate a usual fall population substantially in excess of the winter carrying capacity of the land.

CARRYING CAPACITY: DEFINITION AND DISCUSSION

Winter carrying capacity for bob-white, as used here, was first defined as the heaviest population that a specific environment could be expected to winter [Errington (26)].

In view of the variable interpretations put upon this concept by almost every reader, perhaps it would be well to elaborate upon the subject in more detail.

We admit that there may be a better term than "carrying capacity" to express our meaning. It may be true that our usage is not wholly correct technically. But insofar as it is used in the absence of anything which we recognize as superior, the least we can do in the interest of clearness is to try and point out plainly what we do and do not intend it to mean.

It is especially desirable that there be a minimum of misunderstanding in this respect, for carrying capacity is a property of unique significance so far as bob-white wintering environment is concerned.

Carrying capacity is not calculated on the basis of average survival in a given covey territory from year to year. Just as emphatically, it is not an average of survivals in all observed
territories for 1 year or a series of years. In its simplest form, carrying capacity may be said to denote the upper limit of survival possible in a given covey territory as it exists under the most favorable conditions. This limit has now been found to be more exact for groups of adjacent territories than for single territories. It is calculated on the basis of survivals recorded over a period of years for specific territories or groups of territories [Errington (26)]. Finally, while carrying capacity appears to be relatively constant from year to year for a specific territory or group of territories, it is not the same for all territories or groups of territories.

While data on average survival are certainly of value, they do not constitute a basis for the determination of carrying capacity as herein defined. Carrying capacity refers to a comparatively rigid and non-fluctuating winter survival limit which in nature is not attained every season, but which, nevertheless, effectively delimits higher population ascendencies. Average survival is conditioned not only by carrying capacity at one extreme, but also by variables such as winter emergencies, excessive shooting and incomplete population recovery during the breeding season.

To quote from a recent popular article [Errington (28)]:

“Winter carrying capacity of quail environment may be crudely compared to the capacity of a farm chicken coop. A chicken coop has room for only about so many birds, and if a poultryman has more chickens than his coop can accommodate, obviously he cannot get them all in. If the extra chickens leave the premises and find security in some other poultryman’s coop, which doesn’t happen to be filled up, it may make little difference to them. In the event of visits by predators, the chickens exposed outside will suffer, not the ones secure in coops. Depredations may continue until all of the chickens outside of the coops have been killed or driven away; those properly housed, however, will still be reasonably safe.

“To be sure, a quail wintering territory has not as sharply defined boundaries as a chicken coop, but the analogy is not far fetched. A quail covey range or territory has a combination of food resources and escape cover suitable for an approximately constant number of birds. As chicken coops are built in different sizes, so covey territories occur with different carrying capacities . . . . .

“On the basis of data . . . . it seems that the upper survival limit is almost a fixed property, almost as inherent in the wintering territories as capacity is in a chicken coop. Our hypothetical poultryman could not expect to winter more chickens than he had accommodations for, irrespective of the number with which he might start the season . . . . Similarly, in the case of quail territories, it appears to make little
difference how many extra birds station themselves in a territory, because a limit of only about so many will get by, this limit varying with the individual territory . . . . . . . . .

Whatever may be the net winter survival, for one or more specific seasons or for an average of seasons, a certain environmental inflexibility seems always to operate for the reduction of top-heavy populations to the level of carrying capacity. Starvation and possibly drastic but irregular emergencies of other sorts may reduce populations further.

In nature, the automatic limitation of winter survival to a rather constant year to year maximum has been repeatedly observed in the course of our field studies. Its salient manifestations have been carefully measured, although many details of its mechanism are still lamentably obscure and unyielding to investigation. Survival data from a succession of mild and open winters have been of particular value, in that they have dealt rather consistently with the decline of fall over-populations to the accommodation-capacities of specific environments, thus reducing the likelihood of confusion of the shrinkages attending over-populations with the emergency losses due to blizzards and to starvation precipitated by deep snows.

The definition of carrying capacity may perhaps be restated as the level beyond which simple predation upon adult birds, their own territorial intolerances, and their tendencies to depart from coverts over-crowded with their own or some other species do not permit continued maintenance of population.

The expression "simple predation," or predation upon adult, vigorous birds, is used in contradistinction to what we may call "conditioned predation", the weight of which is felt largely by semi-helpless juveniles, birds weakened by injuries, hunger, or disease [Green and Wade (38)], or those otherwise handicapped individually.

Simple winter predation may at times be conspicuous or unquestionably heavy, but so far as we have been able to measure it, it is chiefly confined to that portion of the population which is in excess of carrying capacity, seemingly irrespective of kinds and numbers of predatory species present. Differences in composition of predator populations studied in connection with the quail observational areas have had no perceptible correlation with quail mortality [Errington (26)]. Insecurity of position of the over-population seems to be the principal factor governing the net winter loss from natural enemies. The population in excess of carrying capacity is dangerously exposed and hence doomed, be there few or many predators.

Conversely, a winter bob-white population within the carrying capacity of its environment shows relatively slight vulner-
ability to predation under the conditions studied, except when the fitness of the population is lowered from some cause. Apart from acceleration of predation loss rates incidental to starvation, crippling from shooting, possibly disease, etc., well situated populations were rarely observed to suffer winter losses from wild enemies at rates exceeding 6 percent per 90 days. Superior bob-white winter densities—up to a bird per 4 acres and doubtless higher—were not known to suffer from predation at proportionately higher rates, provided that the carrying capacities of their environments were sufficiently high to accommodate them properly.

MEASUREMENT OF WINTER CARRYING CAPACITY FOR BOB-WHITE

The most reliable means of arriving at any conclusions relative to the carrying capacity of an area is one of actual measurement. Actual measurement necessitates three things: (1) census work over a period of winters, preferably uninterrupted, (2) separation of emergency winter losses (mainly associated with deep snow starvation and pot-shooting) from losses due to over-population (manifested by heavy predation on unweakened birds or often by departure of coveys), and (3) sufficient ecological stability of environment that the carrying capacity itself will not be subject to wide fluctuations from winter to winter.

Census work that is worthy of the name demands of the observer a certain specialized field technique, a knowledge of quail behavior, and, at times, an almost insatiable thoroughness. It demands also a mental attitude which permits the following up of a particular lead without bias.

We have found that passable skill in winter bob-white census work requires a background of at least one season’s experience in the field under critical supervision and training. In general, we have not found unguided censuses by self-taught observers, hunters, farmers and amateur naturalists reliable. Too often a self-taught observer’s background is so permeated by opinions and part-truths that his observations are unavoidably prejudiced, even though he may be a man of vast outdoor experience.

With some notable exceptions, cooperative quail study projects with institutions and individuals outside of the College have met with only indifferent success. As a rule, the best work of this sort was done by graduate students whose usually scant previous experience was more than counterbalanced by energetic interest and lack of old prejudices. Occasionally, an older man, such as the highest type of deputy game warden, may contribute valuable aid, if he is not more anxious to prove his own ideas than to seek diligently and
impartially for whatever may be true.

The splitting up of the net losses of a winter bob-white population into the various mortality categories demands far greater effort and field skill than making censuses, however difficult the latter may be. Not only must carcasses or remains of missing birds be found, but specific causes of mortality must be ascertained in a sufficient proportion of the cases to permit reasonably accurate conclusions. This necessitates field work of the most intensive kind and an ability to "read sign" that has to be patiently acquired. It may necessitate supplementary work on species, other than bob-white, which may be visitors or co-occupants of the observational area, particularly by means of contemporaneous food habits studies of the principal predatory species.

The third condition for an accurate measurement of carrying capacity is fundamental environmental stability. That is to say, the food and cover combinations should remain in somewhat similar relationships to each other from one winter to the next. Granted that a severe storm may bring about a temporary or even a prolonged upset of bob-white living routine, with possibilities of terrific emergency mortality, its effects may still be essentially measurable. The eviction of established coveys from their territories by irregular but devastating agricultural practices, on the other hand, presents difficulties to correct analyses that may be insurmountable.

To illustrate: In non-glaciated south-western Wisconsin, many farms are small enough to be within the regular range of one or two quail coveys. As the cover conditions commonly remain more or less unchanged for several years at a stretch, the major environmental variations are apt to occur through crop rotation. Nevertheless, since most of the cultivated fields may be small and located in the valleys between wooded hills, the actual accessibility from habitable cover may not differ greatly, whichever field may be in corn, soybeans, small grain, or forage crop one year or another. For many environments of such comparative stability, carrying capacities have not been noted to differ perceptibly over periods of several years.

Although covey wintering territories have been known to maintain an almost incredible year to year constancy of carrying capacity despite environmental changes for either better or worse, this constancy may not be maintained if change takes place on a large enough scale. Central Iowa farm land is nearly all under cultivation, but, because of the large size of the fields, only a small amount is situated near enough to cover (that is, within 50 to 100 yards) as to be habitable for quail in winter. A far smaller proportion furnishes the food and cover combinations requisite to a regularly habitable covert. While ordinary small farm crop rotation, fall plowing, or heavy pasturing of
occasionally cultivated fields may not be followed by extreme fluctuations in carrying capacity for quail, profound environmental changes involving large blocks of land may cause fluctuations of great irregularity and violence, from one extreme to the other. A given central Iowa farm may be well stocked with quail one winter and barren of them the next, according to fortuitous differences in food and cover combinations; hence, it can readily be seen that determinations of carrying capacity are likely to be most accurate when made on lands divided into smaller fields.

WINTER MOBILITY AND BEHAVIOR OF BOB-WHITE POPULATIONS

The bob-white is one of the few species for which the practicality of censusing by direct enumeration has been demonstrated. That direct enumeration may have its limitations should be obvious to anyone of biological understanding; counts may be excellent or worthless, just as any measurement may be excellent or worthless, according to the skill of the investigator and the difficulties presented by the problem.

Direct enumeration of winter bob-white populations is immeasurably facilitated by the relatively sedentary habits of the species at this season, and it should be to advantage to discuss usual and exceptional covey movements in some detail.

After the “fall shuffle” previously described, or the reorientation of coveys in prospective winter quarters, there is likely to be little shifting on a considerable scale except in response to necessity.

During periods of snow, it has been possible to determine that the cruising radii for coveys living under favorable conditions were short, and that the birds could usually be flushed within a quarter mile of the same place at each visit. This observed partiality of coveys for given winter territories has been substantiated in the north by banding results [Errington (18)].

Coveys show a tendency to develop a living routine, which, if safe, they cling to indefinitely. Shooting, attacks by the much feared Cooper’s hawk [Errington (13)] or continued disturbances as by wood cutting may cause pronounced modifications in covey habits but seldom drive the quail altogether out of their territories. The birds usually station themselves in another part of their established range to avoid danger or annoyance, assuming, of course, that other parts of their range are habitable.

Even if undisturbed and well situated a covey may now and then move considerable distances for no apparent reason. One such covey was known to have travelled 1.2 miles in a straight line in 1 day, to return shortly, and thereafter to make no
recognized departures from its regular territory during the greater part of the winter.

Commonly, however, a covey does not move about greatly unless it has to. Hunger is a powerful driving force and may not only lengthen the cruising radius of an established covey in its foraging for food (uninterrupted journeys of a half mile are not unusual for moderately hungry coveys, though usually the quail keep within their regular territories), but may be the cause of chaotic and desperate winter shifting.

The reaction of a covey to a food shortage seems dependent upon the onset and severity of the crisis. Sudden and complete failure of the food supply may drive a covey out of its territory altogether. If the food failure is gradual, the birds may merely spend more time foraging or may starve slowly and passively. Whether the crisis comes on suddenly or gradually, one cannot predict with certainty what the birds will do; they may or may not leave.

Much of the winter movement which takes place on a large scale may be attributed to wandering coveys that have no really suitable place to stay and never have had since fall. These wanderers represent to a material extent the doomed over-population of the year or those evicted by wholesale destruction of habitats, as by burning, plowing, or "cleaning up" of brushy roadsides or fence rows. Some territories are consistently deserted before the winter is over, although the coveys in a shifting state may prove to be worse off than they were even in inferior but established range.

Except for those coveys moving from distinctly uninhabitable or lethal environments and the comparatively minor proportion that safely station themselves in the vicinity of farm yards to feed with the chickens or stock or about the granaries (ordinarily a wise move for an adaptable or an exceedingly desperate covey), widespread winter shifting is not likely to bring any pronounced change for the better for a restless and ill-situated population. Nearly everywhere the first rate environment is already occupied to capacity, and for shifting coveys the poorer grades are not likely to be much of an improvement over those left behind.

The proximity of bob-white coveys in an area seemingly influences movement to a considerable degree, for specific intolerance becomes evident as densities rise past a certain level. The bob-white is gregarious enough to combine in coveys, but ordinarily displays an antipathy toward heavy concentrations.

4. Sometimes the intolerance is inter-specific, as indicated by reactions of bob-white coveys toward concentrations of ring-necked pheasants [Errington (19), (20)].
The fall strife between whole coveys now and then recorded [for example, see Errington (24)] is probably a manifestation of territorial intolerance. This is distinct from the breeding season combats, well described by Stoddard (70). It is possible, however, that most adjustments may be made without a great deal of violence, despite the frequent hostility and combative-ness to be witnessed throughout the winter. The bulk of the evidence seems to indicate a tendency on the part of winter coveys—even when pressed by extremity—simply to avoid coverts that are well populated already.

Rarely have we counted more than 35 bob-whites in intimate covey combination, though we have recorded temporary associations somewhat in excess of this number, largely as a consequence of emergencies. Whether avoidance of overcrowding may be due to compulsion, to instinctive reaction, or to experience (by which much of their behavior is governed) is problematical. Stoddard (70 p. 64) suggests that attacks upon strange birds introduced into bob-white wintering pens on game farms “may lie in an instinctive desire to prevent additional birds from sharing an already over-crowded range.”

In areas sparsely populated with quail, the birds seem to exhibit a greater freedom of movement than do birds of more populous surroundings. Movement may be necessitated by the poor quality of the environment, but this is not wholly explanatory. There may be only a single covey in a large tract of land as a whole uninhabitable for quail, yet the environment may be locally excellent where those few birds live.

COMPOSITION OF THE BOB-WHITE COVEY

Stoddard (70 p. 169) defines a quail covey as “an aggregation of individuals of convenient number (10 to 30), regularly inhabiting an area that provides such essentials as food supply and a sheltering vegetation of favored kinds and in proper abundance.”

It is but a unit of convenience and of no fixed number or composition. It may begin as a family group, but it is not likely to remain as one during the winter, except under conditions in which bob-white populations are so very sparse that additional birds do not occur for miles. Greater or less interchange between neighboring broods and coveys takes place, and as an end result the winter covey may contain young birds of different ages, plus miscellaneous adults, including not only parent birds but also those that were unsuccessful in mating.

Stoddard’s banding studies (70 pp. 169-182) constitute the most voluminous source of data on this subject. Banding records from Wisconsin [Errington (18)] are in essential agreement with Stoddard’s findings, but they indicate, as might be expected, a lessened interchange of birds between winter
coveys. Wisconsin field studies, moreover, have shown, with some exceptions, a greater constancy of covey composition. Coveys in lightly to moderately populated areas of southern Wisconsin are usually made up of the same individual birds for weeks at a time.

The degree to which coveys preserve their identity is partially dependent upon the nearness of other coveys with which they may come in frequent contact. Less interchange is likely to take place between coveys having only occasionally overlapping cruising radii than between coveys living in closer proximity. Stoddard and Errington both found this to be the case.

Even under crowded conditions Errington (20) found some coveys maintaining their identity in a remarkable manner: "As an extreme, one covey of 4 was noted to keep strictly to itself for some weeks, although it shared a territory with another covey of 12. Commonly, small groups like this are absorbed by larger units [Stoddard points this out very plainly, also]. Coveys of 6 to 8 are often found separate, however, where they have plenty of opportunity to combine with other birds. One would hardly expect these small coveys of distinctive sizes and exhibiting distinctive behavior for protracted periods to be composed of any save the same birds.

"It is a common occurrence, too, for small coveys to unite with larger ones (such as one of 8 with another of 12 to form a covey of 20). A recently combined covey is usually weakest at its point of junction; the above would probably split into its component parts (8+12), but not invariably (it may split as 7+13 and 9+11). Sometimes more than two coveys combine, as in a fairly well isolated area at Prairie du Sac, Wis., in 1930-31 where coveys of 9, 15, and 24 coalesced—2 birds lost, 1 gained [influx from outside]—to give at different times [counts of] 30+17; 29+18, 28+19, 27+20; the converse may likewise be illustrated by another Prairie du Sac area in which coveys of 15, 16, and 31 split up and recombined as 10+12+16+24 and in other ways. In these latter instances the exact composition of the coveys could not have been determined except by banding or marking, but the total of associated covey groups was remote enough from those of bordering areas to reduce the chance of interchange with outside birds.

"Splitting and recombining is almost inevitable when a remnant of a decimated covey joins with one already topheavy numerically. If, let us say, a little group of 5 joins a covey of 30, thereby raising the total to 35, which the quail seem to sense as a dangerous or unwieldy concentration, the 35 may split into more desirable units of 15+20, 16+19, etc . . . ."

5. The occurrence of 24 and 31, or exactly half of the respective populations resident at the time, in single coveys is looked upon as a fortuitous coincidence. These examples were selected from many because they were especially clear-cut and were founded upon reliable data.
Some sort of splitting of large coveys is virtually a necessity for resting and roosting, as at these times the birds sit tail to tail in compact bunches. Resting or roosting birds as a rule bunch up in groups located within a few feet of each other, but component groups of the same general covey are often found many yards apart or may go off in different directions. Such separations, frequently noted, are of brief duration, but sometimes the component groups do not rejoin at all; they may even join other coveys or similarly split component groups off other coveys.

With the approach of the mating season in the spring, restlessness within the covey units becomes conspicuous. As early as February, males and females leave the main body of the covey in twos and fours for short periods. By March, there is more and more pairing off, but cold or stormy weather brings the birds back into covey formation. Birds may still be loosely paired and attached to the old coveys, but the flocking habit gradually weakens. April generally witnesses the final disintegration of the covey unit for the breeding season.

To summarize: Prior to the dispersal of birds in connection with breeding activities, the composition and behavior of the bob-white covey under North-central States conditions have shown sufficient regularity and irregularity both to aid and to handicap census studies.

Interchange of birds with neighboring coveys; splitting and recombinations of coveys and covey fragments; daily movements of coveys on account of living routine or random impulse or disturbance; population shifting in search of territories, food, or to escape harassing predators (man included), or for no discernible reason; all these represent departures from static conditions.

It is our opinion, however, that much as winter bob-whites may move within and without definite covey ranges, they rarely move into territory strange to all of the members of the covey. The radius of familiarity of an individual is doubtless of greater significance in delimiting movement than the boundaries of its ordinary territory. In other words, while an insecure covey may show no partiality for any particular territory and may wander far and wide, the probability is that its wandering will be rather definitely confined to a specific area, though that area may be several square miles in size.

With all the exceptions noted, the winter bob-white at low to moderate densities is still a comparatively sedentary species. It usually does not move nearly as much or as erratically as its occasionally demonstrated mobility and its physical powers would permit. By and large, it is a species especially amenable to direct enumeration census studies by competent observers under favorable conditions.
DIRECT ENUMERATION CENSUS TECHNIQUES FOR
BOB-WHITE

A brief discussion of winter census techniques has been published in connection with the Wisconsin studies [Errington (20)] but, in view of subsequent experience and the constantly growing demand for information, we believe that it would be advantageous to revise and present our material on this subject in greater detail.

Some preliminary remarks may be in order. In the first place, reliability of census figures—assuming that the observer is competent—varies roughly with the presence or absence of tracking snows, with the time spent on a given area, with the size of the area under observation (up to manageable limits), and inversely with the density and the insecurity of the population.

All snows are not tracking snows; those of icy consistency glazed over by sleet or by sun do not register the tracks of a bird weighing less than a half pound. A drifting snow or one bespattered by falling icicles and water drops also is not the best for tracking purposes.

Thaws may soften much crusted and hard drifted snow, however, so that it furnishes an excellent register for tracks, especially of birds active during the warm part of the day. Imprints made in wet snow are often preserved by night freezing until they have been melted out the next day, and even then their traces may be clearly distinguishable. Thaws may not aid, however, in the censusing of coveys that restrict their activity more or less to the morning when snow surfaces may be impervious to their tracks because of freezing of the wet snow during the night.

The amount of time necessary to keep an area under adequate observation depends upon the difficulty experienced in obtaining censuses and upon what may be happening. If the studies are intended to be really intensive, covey groups should be visited every week or two for the duration of the winter—provided the birds are getting along fairly well and that the counts at each visit are reasonably satisfactory. If the investigator is having trouble in finding the birds or their tracks, or if current developments (heavy predation, poaching, population shifting, starvation emergencies, etc.) necessitate closer observation, it may be well to make visits every day or two, at least during such periods of confusion and crisis.

Sometimes it is necessary virtually to comb an area over and over again to extract the significant details of the ecological drama which may be taking place. We may say parenthetically that an observer learns with experience to cover an area with a maximum of thoroughness and a minimum of disturbance of
the birds themselves and a minimum of interference with the
natural order of events.

In general, areas or samples chosen for observation should
be large enough to reduce the likelihood of complications
through interchange of birds with uncensused coveys outside,
yet small enough to be within the power of the observer to
handle. We have found that a tract of land 1 square mile in
area is about as small as may be profitably kept under observa­
tion, and this unit is often too small for reliable study when
much population movement takes place. As an upper size limit,
we believe that 5 square miles is enough to try to take care of in
one block.

Large rivers, lakes, solid tracts of forest or woodland, wide
expanses of cleanly cultivated land, suburbs and towns, or
other physical features may provide virtual barriers to winter
bob-white movements and may be of great aid in census work if
they bound one or more sides of an observational area. Fre­
quently, actual studies demonstrate that many areas are so
effectually bounded by environment inhospitable to quail that
practically all winter influx and egress is restricted to a few
places that may be watched. For example, habitable winter
quail environment in much of central Iowa may be limited to
interrupted stretches of brush-bordered creeks, and may thus
serve somewhat as islands in the partial isolation of local
populations.

In general, the higher the bob-white densities in a given
area the more difficult it is to keep track of interchange
between coveys and the increasing amount of splitting and
recombining. We have, for this reason, found ourselves quite
unable to census with real accuracy populations in excess of a
bird per 4 acres.

At a level of a bird per 4 acres, while local concentrations of
50 to 60 birds in constantly mixing coveys may frequently be
found on a 40-acre tract, these concentrations are likely to be
separated from other covey groups by unoccupied stretches of
perhaps a half mile or so. Under favorable conditions or by dint
of persistent and well directed effort, it is usually possible at
some time or other to secure nearly simultaneous check-ups on
the constituent coveys of such semi-isolated though densely
localized population groups.

At higher densities, there is less likelihood of finding semi­
isolated groups small enough to be censused in the necessaril­
short time to prevent results being influenced by covey inter­
change and mixing. If a group of coveys is especially subject
to mixing, an investigator should strive to complete his
censuses within a space of 2 or 3 hours or at the most on 1 day's
tracking snow. Where one strong quail environment grades off
into another in continuous succession, there is slight chance of
being able to obtain accurate counts on all closely neighboring coveys before mixing occurs.

Hence, well-handled censuses, which may be accurate to a bird for low and medium densities, become more and more inaccurate as densities rise, until for the higher quail levels of a bird per 1 to 2 acres they may not at best be more than careful approximations.

It goes without saying, moreover, that securely situated populations are far more easily and reliably censused than those that do a great deal of shifting in response to food shortage, over-crowding, or eviction from former habitats. Indeed, we have found the chaotic censuses of some populations quite beyond our ability to straighten out, irrespective of the significance of the ecological phenomena which this restlessness may have reflected.

**TECHNIQUE OF TRACK COUNTING**

Track counts are of the greatest usefulness in bob-white census work, especially if checked by flushing and counting the birds at the end of fresh covey trails. Usually track counts are obtained in snow, but under exceptional circumstances in sand or mud.

As pointed out in the preceding section, the efficacy of track counting as a census method is conditioned by the distribution or the state of the snow. The difficulty of obtaining track counts may be further increased by the absence of snow at strategic places or by daily accumulation of tracks in an indecipherable maze.

Erratic behavior of the quail themselves may add to the difficulties. Well-fed coveys occasionally lie up without moving during the first day of a fresh snow, or do not venture forth until late. In the event of an early morning snowfall, some coveys may feed so soon after it becomes light that they may not leave any tracks or only tracks so dimmed by the subsequent snow as to be uncountable.

Deep, fluffy snows cause the quail to fly instead of run from one place to another, or to leave a trail that is a bewildering series of short flights and shorter runs.

Snow of this consistency accentuates the tendencies of coveys to run along in single file in packed trails. Bob-whites also have a tendency to run in single file or in a massed trail when gently alarmed, as by approaching people. For this reason, an observer should be careful not to obliterate spreading tracks with his feet until he has obtained a reliable count, as the covey trail may grow worse the farther he follows it.

The best track counts can be made at points intermediate between a covey’s roosting or resting spot and its feeding ground. At some point en route the covey trail usually widens
out enough to permit recognition and counting of the individual trails (fig. 2). When the covey trail is partly massed and partly open, it is sometimes possible to make accurate counts of a portion of the covey at one point and of the remainder at another (fig. 3). Where individual trails may be grouped in twos, threes, fours, etc., for part of the distance, it may be advantageous to block off groups for separate scrutiny and analysis.

It is imperative to watch the covey trail carefully, for a lagging or an impatient bird may take wing and so leave no tracks over part of the route. Repeated counts along the trail (especially the trail of a large covey running in loose snow) are necessary to reduce likelihood of error.

The directions of individual trails must be watched constantly, as birds have a way of doubling back more or less in the course of leisurely travel or when alarmed and undecided (fig. 4). A single trail reversed but undetected may result in an over-count of two birds. Commonly, satisfactory counts are difficult to make in trails where there is much back-tracking and massing (fig. 5). If the back-tracking is limited, and the pattern is open, back trails and forward trails may simply be cancelled out, one for one.

We have found chances best for making good track counts on the margins of roadides, on frozen creeks and sloughs, at the edges of fields and open spaces where coveys may cross smooth stretches of snow in spread-out formation. Irregularities in the trails where birds have either taken wing or have alighted as strung-out coveys should be considered in census work, as well as trails of coveys incompletely assembled after having been split or scattered. Counts on feeding grounds are suitable if the coveys progress in some particular direction without too much back-tracking or zig-zagging.

An investigator finds increasing familiarity with individual covey habits of tremendous assistance in locating tracks or birds without unprofitable search. Although very thorough investigation should be made occasionally of all parts of an observational area, quail-occupied or not, in practice, a hurried survey of favorite coverts may be all that time allows, especially if the hour is late in the day or if an ephemeral tracking snow is rapidly melting.

Certain strips of fencerow brush, certain hill slopes, certain clumps of gooseberries, fallen trees, etc., may be preferred for resting or sunning. There may be special bushes under which a covey may like to scratch for fallen fruits. Other birds may prefer habitually frequented sites for dusting or replenishing grit. Others may regularly use such “highways” as ditches, fences or ravines, or may approach feeding grounds from a particular direction, or may develop similar idiosyncracies of which legitimate use may be made in census work.
Fig. 2. Trail of a covey of 9 quail, countable in places.

Fig. 3. Partly massed and partly open trail of a covey of 13 quail.
Fig. 4. Trail of a covey of 14 quail, illustrating some back-tracking and irregularity of movement.

Fig. 5. Difficult trail in which the tracks of at least 13 birds can be made out.
The danger of short-cuts in technique is that they may be conducive to hasty inspections and carelessness. The judicious use of short-cuts, however, may add to an investigator's efficiency; in directing his course to include the most likely coverts, he does not have to ignore those that may be less frequented, or assume that they are not occupied.

**FLUSH COUNTS**

Counts of flying (or flushed) birds are relied upon chiefly during winters when tracking snows are of rare or irregular occurrence, or early in the season before tracking snows come. Flush counts are also used during snow periods to verify track counts.

In making flush counts, an investigator is beset by two obvious difficulties: First locating coveys, and second obtaining accurate counts of the birds.

Locating coveys without the aid of snow may be greatly facilitated by the use of a trained dog [Wight (76)]. Dog-users, however, may over-estimate the efficiency of their favorite dogs and may depend too much upon them. Excellent as may be a dog's nose and "quail sense," it by no means follows that there are no more quail to be found on a given area simply because the dog cannot locate any more, vehement contentions to the contrary notwithstanding.

A good dog if properly used may unquestionably be of valuable help under snowless conditions, but the disadvantages of using a dog as well as the advantages should be recognized. A good dog cannot make up for lack of skill and diligence in the human observer. Skill in both dog and man constitutes the ideal combination, but of these two the skill in the man is more important. Indeed, it is our opinion that a truly skilled field man may make a better all-around "bird dog" than the dog itself, despite the fact that he does not have the dog's ability to find birds by scent. A skilled field man can read the story of quail droppings, dust baths, feathers, tracks and other "sign" when it is too old to interest a dog at all.

There are times in winter census work when a dog should not be taken into the fields, particularly during tracking snows when a dog may by his own tracks mess up covey trails at strategic places so that counts cannot be made. The investigator himself may have to watch where he steps amid the individual trails, and dogs are seldom completely controllable. On other occasions, dogs may cause quail to "freeze" when it may be desired that they flush freely.

On the subject of flush counts we may quote again (20): "A flush count is quite reliable for use with small coveys (5 to 10) and with those of moderate size (up to 20) where the quail fly well spread out and are not continually shifting places."
A covey leaving a patch of thick cover such as a mat of creeping juniper in a steady succession of singles, twos, and threes can often be readily counted. Where a large flock bursts into flight as a compact mass, it is virtually impossible to obtain an accurate count, although an investigator, through increasing familiarity with coveys, learns to estimate size within a bird or two by general appearance in the air.

"Flush counts are of scant utility if the birds have been disturbed and scattered a short time previous. Premature attempts to reflush for count a covey previously flushed and marked down are also unprofitable. Immediate reflushes are invaluable, however, in detecting weak individuals in the covey, for underpar birds may have the strength for a vigorous first flight but little more.

"Censuses of an area were planned in such a way that flushed coveys were encouraged to alight in territory already covered, so as to obviate the chances of their being counted twice or confused with other birds. In actuality, things do not work out as smoothly as planned, but the quail, through the proper approach of their favorite rendezvous, may often be guided into flying about where desired."

It might be added that flush counts present certain other pit-falls that need to be guarded against. Sometimes two or three birds flush apart from the main body of a covey, and, if these rise behind or far to the side of an observer, he may not see them. Some members of a covey may have their flight concealed by obstructions to vision, low visibility and so forth. Incompletely assembled coveys and individual members disposed to hide rather than to fly when approached are a source of error.

No one should be too sure of the census figures secured from a single visit, even when aided by snow. Repeated visits and critical evaluation of results are essential for accuracy.

Running counts may be discussed in the same category as flush counts. They may or may not be reliable, according to whether all of the birds pass directly in the observer's line of vision and are noticed before some birds disappear from view. Counts may be confused by birds running back and forth, by two or three dashing past abreast, or by lagging individuals becoming alarmed, to turn back or veer to the side unseen. Roadsides, open spaces, hollows in ditches, erosion gullies, or ravines offer opportunities for running counts. Birds en route to or leaving feeding stations may frequently be counted with comparative reliability and ease.

COUNTS WITH THE AID OF COVEY RESTS AND ROOSTS

Counts of the body impressions on roosts are much less dependable than any of the census techniques thus far dis-
cussed. This method should be used sparingly and only under the conditions best adapted to it, and where even an undependable method is better than none. We have found it most useful in the checking up of coveys of approximately known size when track counts were impossible and the birds could not be located or satisfactorily counted in flight.

When a covey flushes from a roost after having been partly snowed over during the night, clear imprints of individual breasts may sometimes be evident. Imprints of breasts may sometimes be distinguished also when quail roost on frosty nights in soft, thick grass. The great drawback to the method, aside from the indistinctness of body outlines, lies in the possibility of roosting covey groups rearranging themselves in the night. Relative quantities of droppings corresponding to imprints may give a clue as to whether or not rearrangement has taken place.

We have been unable to use the quantity of droppings on a roost as a positive index to the number of birds, as the quantity of droppings is dependent both upon the diet of the birds and the length of time that a covey has spent upon a particular roost. Night flushes of coveys by mammals, interruptions in feeding of individual covey members during the day, or food crises on account of snow or ice storms, introduce too many variables.

Daylight resting places, however, seem to offer a trifle more promise to an investigator. The birds bunch up for even more variable periods of time than they do at night, but the bunched group tends to be less compact, and feces from a few individuals may frequently be detected in distinct little piles, although the majority of the droppings may be scattered over a space of 2 or 3 square feet.

If the evidence indicates that these little piles represent the droppings accumulated from the first birds to station themselves in any definite position during the time that the covey was resting, and if each of the distinctly separate piles contains about the same number of droppings, then it may be possible to calculate the approximate number of birds in the resting covey by dividing the total number of droppings by the average number per separate individual pile. For instance, if the total number of fresh droppings is 67 and the counts for three distinctly individual piles give five, five and six or an average of five, the total of 67 divided by five establishes the number of birds in the covey in the vicinity of 13.

We have found, by checking calculations of this sort against actual censuses of the coveys which had been on the rests, that our likelihood of error ordinarily does not exceed 20 percent. This percentage is far too high for work that demands precise survival figures, but it is often very useful to determine, when
birds can neither be found, nor censused, whether a given territory is occupied by many birds or few.

INTERPRETATION OF CENSUS DATA

Interpretation of bob-white winter census data may be comparatively simple or may be beset by the most formidable of difficulties. The difficulties are usually in direct proportion to the density of the quail population studied and the amount of covey interchange and shifting which have taken place. Further difficulties may be presented by lack of data at strategic times.

When the total quail population of an isolated piece of land was only, let us say, a covey of nine birds at the beginning of the winter, of which eight were known to have survived and the other was known to have been killed by a horned owl, the investigator may regard his data with a certain confidence, so far as they go. But when the season's notes show a succession of coveys appearing and coveys disappearing and census fluctuations for territories regularly occupied as well, the fragments of evidence have to be fitted with care if a truthful picture of what happened is to be reconstructed. Of course, if the data are too chaotic, any refinement of deductions would be spurious, and the most one could extract from them would be broad and evident generalizations.

Let us consider a fairly complex example of raw but essentially workable wintering data from part of an observational area near Prairie du Sac, Wis., season of 1931-32.

Figure 6 depicts the rough outline of a series of occupied bob-white ranges, themselves more or less contiguous but separated by significant distance or by effective barriers from occupied territories outside. The general covey headquarters are designated by letters, and the locations of outside coveys by asterisks. The asterisk-indicated coveys were sometimes near, but their territories did not conspicuously overlap those of the coveys to be considered, nor was exchange of birds known to have occurred within the period covered by the present data.
For territory “A,” counts of 14 were made on Dec. 12 and Dec. 22. From Jan. 10 on, the birds were no longer to be found here.

For the territory adjacent to the east, “B,” the count on Dec. 18 was 18. On Jan. 10, coincident with the disappearance of the covey of 14 (“A”) on the west, the count was 32, a gain of 14. This certainly gives the basis for a good guess as to what happened.

On Jan. 16, 32 birds were again counted, but as split up coveys of 18 and 14. The inference is plain that the 32 birds had separated into their original covey groups, although they were now occupying the same range.

On Feb. 3, 14 were found and the whereabouts of the other covey was known, but the latter couldn’t be flushed. By Feb. 10, the arrangement was a little different: 15 and 17; Feb. 25, the same. On March 12, the count was 15 and 15, which, as a final figure could indicate the loss of two birds. The suspicion of mortality, however, was partially dispelled by locating a covey of 17 on March 19; and on March 23, the full 32 were present, but now arranged as 9 and 23.

Territories “A” and “B” furnish data almost ideally interpretable, since the interchange was confined to only two coveys in the first place, and since these coveys were closely adjacent and observable with comparative ease. The situation also was not complicated by much irregular movement or by mortality.

More complex are the data from territory “C,” and in the absence of supplementary data from territories outside, it would be hopeless to try to do much with them.

On Nov. 1, the count was 19 for “C”; on Nov. 18, the birds couldn’t be found; on Dec. 9, there were 14. So far, the data are in a veritable muddle and would likely remain so were it not that territory “H,” adjacent to the southeast, was known to have gained about five birds in the interim. Had territory “H” not been under observation at the time, we could not have made an intelligent guess as to whether the missing birds had been killed, had moved out, or whether the territory had not been abandoned by the original covey, later to be occupied by an entirely different one. The story is not yet completely clear, but the evidence pieces together rather nicely.

Subsequent counts showed no change until Jan. 5, when the covey gained one bird, thereby bringing the number up to 15. The gain was soon lost, for by Jan. 9, the covey was down to 13; the newcomer had probably joined for temporary convenience after some scattering of its own covey, later to go back where it belonged.

On Jan. 28, covey “C” was down to 11; Feb. 6, the same; 10 on Feb. 17; and 9 from Feb. 27 to March 16. The shrinkage
from 14 to 9 probably in the main represents mortality, though our field data give us little answer as to specific causes. Gradual decline is much more apt to indicate mortality than sudden disappearance of a number of birds at a time.

Next, we have data virtually impossible to interpret correctly without thorough familiarity with the situation as a whole.

In territory "D" about 22 birds were counted on Oct. 30, never to be found there again.

The same number were counted Dec. 8 in territory "E," a territory previously unoccupied. The birds were never found here again either.

Territory "F," likewise previously unoccupied and soon deserted, had 26 birds on Dec. 18.

Finally, a large covey appeared in the previously vacant territory, "G." The first count, on Jan. 10, was 23. The covey elected to stay here, but lost steadily from the beginning. Following counts were: 22, on Jan. 16; 16, Feb. 3; 13, Feb. 10; 8, Feb. 25; 7, March 3; 4, March 12; and but 2, March 23.

It was apparent, from scrutiny of the current census data from surrounding territories and from prospective though unoccupied quail habitats, that the territories "D," "E" and "F" simply represented stopping points in the wandering of the covey which eventually stationed itself at "G," at a distance of nearly a mile and a half from the place where first noted. The soundness of evidence as circumstantial as this is dependent upon the quality of the data pertaining not only to that part of the population which is shifting, but also to that part which is comparatively sedentary and established.

The losses shown by territory "G" represent mortality from predation, terrific and conspicuous. The gradual, constant shrinkage alone would indicate as much, even had the remains of birds not been scattered all over the territory and had not the winter's killing been traced almost completely and exclusively to great horned owls.

Later on in this bulletin, the interpretation of data will be carried on much farther, and the recorded lethal history of territory "G" will be presented for analysis, season by season.

TECHNIQUE OF TRACING MORTALITY

It has been found advantageous to locate the coveys of a prospective observational area rather early in the fall. Even before reliable censuses can be taken, the whereabouts of coveys may often be ascertained by listening for quail calls and by the reading of "sign" from roosting and resting spots, scattered droppings on feeding grounds, dust baths and feathers.

It is plain that the more nearly absolute a census, the greater
will be its value in determining whether coveys are suffering losses. The disappearance of a bird from a suitably isolated covey or group of coveys (with no subsequent reappearance or no corresponding gain by surrounding coveys) may be accepted as a strong indication of mortality, but the investigator should not be so easily satisfied. His next step should be to search the environs for remains of the missing bird and for explanatory "sign."

In many instances (perhaps 50 percent, under favorable conditions) in which birds were known to drop from observational coveys, we have been able to piece together fairly good evidence as to what happened. Our fortunes, however, in tracing the causes of mortality have vacillated from one extreme to the other. Practically all birds missing from some coveys have been accounted for, while in others the majority of disappearances could not be solved. In general, the completeness of the observational data which an experienced observer obtains from an area varies with the time spent.

It is also possible to trace some types of mortality with far less difficulty than others, but the activities of scavengers are a major source of confusion.

Large and medium sized slow hawks, such as marsh hawks, red-tails and rough-legs, and such enterprising mammalian predators as foxes, house cats and minks are constantly feeding on carcasses, including those of quail, which they may have killed but which they more likely found dead. Prey in possession of or eaten by Cooper's hawks or great horned owls commonly represent kills made by those predators. Evidence of crows, skunks, oppossums, dogs and meat-hungry rodents about remains of adult quail almost without exception denote scavenging.

Feather "sign," in the case of the death of a bird no larger than bob-white, does not long remain conspicuous. It may be completely hidden by a light fall of snow or may be made very difficult of detection by wetting, as by rain or melting snow and ice. Wind action, falling and drifting leaves, and mice (which have been known to carry off quail feathers for nest lining) may destroy the evidence in a short time. Unless the same ground is covered every 2 or 3 weeks, feather remains which might definitely account for missing birds may easily be overlooked.

Relative to the pitfalls attending the interpretation of predator kills, a few paragraphs may be directly quoted [Errington (14)]:

"Of fundamental importance to those carrying on a life history study of a given species is the ability to read sign when a kill of that species is found. This ability is acquired slowly and never can begin to approach perfection, if for no reason other than the imperfection of the sign itself. Always must
the investigator watch himself, lest he find out things that aren't true.

"Perhaps it would be in order to review a specific incident. On December 24, 1930, the remains of a quail were seen in a railroad ditch south of Madison, Wisconsin. The sign was two days old. An empty shot-gun shell lay on the grade sixty feet from the quail and there were two wads on the snow between quail and shell. No shot pattern could be located. Cat tracks were noted about the quail remains, and it was obvious that the cat had partaken thereof. A search in the snow brought up a portion of a quail skull, with marks of two canine teeth where a piece had been bitten off. The tooth marks were too close together for cat. To the side of the track-beaten space were rather indistinct prints of mink. The canines of a mink skull checked with the marks on the quail skull. But along with the quail skull a wing had been dug out of the snow—a wing showing the typical clean plucking of an accipitrine hawk. Since a wintering Cooper hawk had been flushed on December 20th, from a warm quail killed out of a neighboring covey, the evidence was now about as clear as circumstantial evidence ever is.

"This kill, fairly fresh and rendered conspicuous by snow, is illustrative of how in one way or another the fleeting records of the wild fade into illegibility. Suppose that the wing had disappeared, or both wing and skull? Suppose that the kill had not been seen until days later, and the site had been inspected in the meantime by . . . . . . other flesh-eaters not averse to scavenging when that is easier than hunting? Suppose that the kill had taken place in summer, a week previous to discovery, and rains, putrefaction, maggots, ants . . . . had had their part in the obliteration of the story?"

The prompt discovery of a dead bird, before scavengers or weather have blotted out the "sign," is therefore a substantial step toward diagnosis of the cause of mortality. Profitable places to look over upon the disappearance of birds are recent roost sites, fencerows, the borders of brushy cover, the ground beneath large or vine-entangled trees and any likely retreats of suspected predatory species.

Starving bob-whites found dead in cold weather leave a story that can be read, as well as do fresh predator kills. If a predator kill is not distinctive enough, it may conceivably be checked up by means other than by "sign reading," especially where remains may be retrieved later, as from raptor nests or pellets. Familiarity with the food habits of the quail coveys in horned owl hunting ranges has been of aid in tracing unbanded victims to their coveys, on the basis of undigested quail food contained in the pellets [Errington (14)].

The normal shedding of quail feathers on roosts or rests
should not be mistaken for evidence of mortality. Flight feathers and small feathers attached to particles of skin, on the other hand, are much more significant. Indeed, one may sometimes find, on the primaries of plucked prey, outlines of raptor beaks sufficiently distinct and characteristic for identification. In the majority of instances, unfortunately, there do not seem to be imprints which one would be justified in accepting as wholly diagnostic. Bill marks of the larger raptors we have found to be most recognizable.

If the carcass is that of a freshly killed quail, one may frequently identify the work of a specific predator or predator group, but one should bear in mind that the technique of a predator species in handling prey is by no means uniform. Foxes and house cats bite off and leave the wings of their victims. Wings roughly plucked and heads gone may indicate horned owls or large hawks; if the prey is eaten by hawks, the stronger bones of breast and shoulder girdle are likely to be left, whereas horned owls with their powerful beaks shear through bones and flesh alike, and often leave nothing after the first meal except hindquarters. Marsh hawks and Cooper’s hawks pluck the primaries and leave the head sometimes intact, sometimes partly eaten. These two have a common habit of eating the flesh from the upper breast first; but much cleaner plucking of the wings is an accipitrine trait—although a small accipiter may not attempt any wing plucking. Stoddard has found the Cooper’s hawk trait of swallowing the legs of a quail victim after decapitation to be perhaps more general than we have observed in the North. Viscera may be relished or discarded, according to the taste of the individual predator.

The differentiation between carrion and killed prey is extremely important in field studies and in the correct interpretation of data from predator stomachs, etc. It may, moreover, be extremely difficult if not actually impossible to do, under many circumstances. Generally, bloodiness of tooth or talon marks indicates a kill. The presence or absence of connective tissue about the base of scattered primaries may be of some assistance in indicating whether they were pulled from a warm kill or pecked loose from a cold carcass. Those portions which have been eaten may provide the best lead in evaluating the evidence, as some parts of a fair sized carcass are less preferred or are seldom eaten except when cold. For example, if a hawk stomach contains nothing except the tail feathers, synsacrum, and bony fragments ordinarily not eaten, one may reasonably judge that there wasn’t much left of the carcass when the hawk started to feed. Of course, unanswered questions are always arising as to whether material eaten as fresh carrion was found dead in the first place or represents killed prey to which a later return was made.
Other leads may be helpful, such as the site of killing or picking or eating, probabilities based upon intimate knowledge of local predatory species, habitual and adaptive behavior of the quail coveys preyed upon, and sundry minor clues; but, in the absence of anything indubitably characteristic, one should not try to come at once to definite conclusions. One should never be hasty in the interpretation of evidence, for it is very easy to record opinion as fact. Carefully written descriptive notes, however, have a permanent value which is more than likely to be enhanced by time and by maturity of experience.

MORTALITY FROM POACHING

While feather evidence is usually to be found when wintering quail suffer mortality—though the “sign” may be so poor that it may only confirm the loss of a bird—a notable exception must be taken into account where human poachers have been active. Often there is little to point to shooting except the vanishing of birds, or perhaps a crippled or killed bird overlooked by the hunters.

Occasionally, one finds where a quail has been shot on the ground or where a handful of feathers has been cut off or torn out by a shot charge. Two or three or a half dozen birds may suddenly be gone from a well established covey; wild-flushing remnants of coveys formerly tame may be encountered; there may be gossip about the neighborhood; but the work of the poaching hunter is exceedingly hard to trace down with any definiteness.

Even more difficult to trace down is the work of quail trappers, unless one finds the actual trap or its former site. Quail are at times easily attracted to certain places by feed and are readily caught in wire cage traps of various designs. Whole coveys or the greater part of whole coveys may now and then be caught in one trap at the same time.

It is apparent that quail trapping on an area might invalidate data from many covey territories. On the whole, however, we have no reason to believe that undetected shooting or trapping has significantly reduced winter populations on our best observational areas. Despite the reduction or total disappearance of certain coveys under suspicious circumstances, we have found that many covey disappearances without trace may simply signify movements and that the birds may be relocated if enough searching is done.

The occasional propensity of acorn-feeding coveys to range in solid blocks of wooded hills, or of coveys to station themselves near the centers of large cornfields for varying periods of time, may be a cause of confusion to an investigator, especially subsequent to the disappearance of those coveys from coverts previously occupied with regularity. Release of an extensive
food supply from snow or ice by a mid-winter thaw may induce rather widespread covey movements, notably after a population had been confined to definitely restricted habitats because of prolonged severe weather.

**PART II. SURVIVAL DATA**

**EVALUATION OF WINTERING DATA**

During the first three winters of the Wisconsin quail investigation, Errington, aided by Albert J. Gastrow of Prairie du Sac, Wis., located for study approximately 2,650 birds in 155 coveys. Of these birds, about 1,600 were kept under regular observation, roughly: 400 from October, 1929 to March, 1930; 500 from December, 1930 to March 1931; 700 from December, 1931 to March, 1932. Particular attention was paid to the influence of food, cover and predation upon winter mortality; and miscellaneous factors bearing upon the problem were given the consideration warranted by their apparent importance.

In the first winter of the Iowa cooperative studies, 1932-33, Errington and Hamerstrom and cooperators in Wisconsin and Iowa, located 84 coveys totalling about 1,250 birds, of which nearly 900 were kept under regular observation from November to March.

The field studies for the winter of 1933-34 were conducted on an extensive scale and were checked by a comparatively small amount of intensive work. Errington, Hamerstrom and Deputy Game Warden C. H. Updegraff (Iowa Fish and Game Commission) obtained data of some sort on 453 coveys totalling about 6,450 birds. Only about 580 wintering quail were regularly observed (most of these by Gastrow), according to standards acceptable for really reliable data, and those from October to April.

During the last season, 1934-35, renewed emphasis was placed upon intensive local studies, and about 870 birds were kept under regular observation out of the total of about 1,300 in 110 coveys upon which some data were secured.

Altogether, then, from 6 years study we have more or less data on about 11,650 quail beginning the winter in about 800 coveys, of which the data on nearly 4,000 birds may be said to be superior. Of the 11,650 total, about 7,750 were Iowa birds studied on 29 areas; the balance were birds on 15 areas in Wisconsin and 2 in Minnesota.

For data, which we evaluate as superior, we believe that the possible error in census figures rarely exceeds 5 percent and in a majority of instances is decidedly lower than that, ranging down to complete accuracy. Exactness in census figures, how-
ever, should not be confused with exactness in mortality determinations. It is one thing to discover that birds are missing from a covey or territory and another thing to establish clearly the cause of their disappearance.

The winter survival data from specific covey territories or groups of adjoining territories may for analytical convenience be separated according to their reliability and to the degree to which they are affected by complicating variables. All numerically reliable data obtained from identical territories under observation for two winters or more are presented. Data are placed in different reliability brackets on the basis of the technical criteria by which they may be judged, not on the basis of anything they may seem to prove or disprove.

The predominance of Wisconsin over Iowa data in the tabulations is marked, although we have had greater numbers of birds under observation in Iowa than in Wisconsin. It simply happens that bob-whites have been far more accurately censused under Wisconsin conditions and that many of the Wisconsin territories have been under regular observation for longer periods of time. Wisconsin bob-white populations and environments alike have on the whole shown more relative stability during the years of these researches, and hence have been more productive of scientifically acceptable data on maximum winter survival.

**SURVIVAL DATA—FIRST CLASS**

(Data from more or less regularly occupied territories bounded on all sides either by territories similarly under observation or by wide quail-vacant spaces or physiographic features serving as barriers to winter movement; data relatively uncomplicated by starvation emergencies or by heavy losses occasioned by factors other than predation or egress.)

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>17 on Dec. 4</td>
<td>17 on Feb. 15</td>
<td>No loss</td>
</tr>
<tr>
<td>1930-31</td>
<td>23 on Dec. 21</td>
<td>17 ? on Mar. 15</td>
<td>Predation; some shooting</td>
</tr>
<tr>
<td>1931-32</td>
<td>11 on Oct. 24</td>
<td>7 on Mar. 2</td>
<td>Probable predation, but atypical</td>
</tr>
<tr>
<td>1932-33</td>
<td>21 on Dec. 7</td>
<td>17 on Mar. 25</td>
<td>Predation; auto traffic</td>
</tr>
<tr>
<td>1933-34</td>
<td>27 on Oct. 22</td>
<td>18 on Mar. 29</td>
<td>Mainly egress</td>
</tr>
<tr>
<td>1934-35</td>
<td>11 on Nov. 12</td>
<td>16 on Mar. 25</td>
<td>Influx; much interchange</td>
</tr>
</tbody>
</table>

Of the final counts for territory number 1 (table 1) on consecutive years (17-17 (?) -7-17-18-16), the substantial loss from predation of 4 out of 11 for 1931-32 when the territory was only partly occupied represents the probable mortality of unusually immature birds. The original covey on Oct. 24 was made up of an adult cock and 10 very backward young in no way equal in winter survival potentiality to adult birds.
TABLE 2. TERRITORY NO. 2—LAKE WINGRA, MADISON, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>37 on Dec. 21</td>
<td>23 on Mar. 28</td>
<td>Mainly starvation</td>
</tr>
<tr>
<td>1930-31</td>
<td>38 on Dec. 20</td>
<td>32 on Mar. 29</td>
<td>Predation</td>
</tr>
<tr>
<td>1931-32</td>
<td>33 on Jan. 4</td>
<td>29 on Mar. 11</td>
<td>Predation and cold</td>
</tr>
<tr>
<td>1932-33</td>
<td>33 on Feb. 14</td>
<td>33 on Mar. 29</td>
<td>No loss during observational period</td>
</tr>
</tbody>
</table>

All but one or two of the birds of territory number 2 (table 2) lost during the season of 1929-30 were lost because of late winter starvation. Had it not been for this emergency, the winter survival would have been in the vicinity of 35. In 1931-32, a cold snap was attended by the disappearance of two birds, possibly in poor condition. In 1932-33, while the period of observation showed no loss, evidences of previous pressure of great horned owls indicated that the population had been reduced thereby to the 33 birds, which seems to represent a level of comparative security from winter predation. The majority of the 1932-33 observations, both at Lake Wingra and University Hill Farm, were made by H. G. Anderson of Madison, Wis.

TABLE 3. TERRITORY NO. 3—UNIVERSITY HILL FARM, MADISON, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>10 on Oct. 25</td>
<td>0 on Jan. 26</td>
<td>Egress and freezing</td>
</tr>
<tr>
<td>1930-31</td>
<td>22 on Jan. 6</td>
<td>19 on Mar. 17</td>
<td>Egress</td>
</tr>
<tr>
<td>1931-32</td>
<td>16 on Jan. 9</td>
<td>16 on Mar. 19</td>
<td>No loss</td>
</tr>
<tr>
<td>1932-33</td>
<td>Covey evicted by agricultural practices</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

During the winter of 1929-30, three birds of territory number 3 (table 3) simply shifted to an adjacent territory, but the remaining 7 were apparently lost through what could best be classed as a freak accident—chilling and freezing in good flesh after their plumage had been saturated in sub-zero weather by steam from a manure pile upon which they had roosted. A temporary influx of 13 from territory number 37 had occurred by March 23.

The eviction of the 1932-33 birds was due to the plowing under or removal, in connection with farm routine, of practically the entire food supply available in the territory.

The carrying capacity for quail of number 3 and adjacent territories was apparently lowered in 1930-31 and 1931-32 by a rise in the pheasant population. A mixed stand of 47 quail and about 30 pheasants was noted in 1930-31, and a stand of 26 quail and about 50 pheasants in 1931-32, totalling in the vicinity of 77 and 76 gallinaceous birds, respectively, for the two seasons on the 200-acre observational tract as a whole [Errington (26)].
TABLE 4. TERRITORY NO. 4 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>15 on Jan. 4</td>
<td>14 on Feb. 16</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1930-31</td>
<td>20 on Dec. 22</td>
<td>20 on Mar. 30</td>
<td>No loss but see text</td>
</tr>
<tr>
<td>1931-32</td>
<td>19 on Nov. 10</td>
<td>15 on Mar. 23</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1932-33</td>
<td>18 on Dec. 9</td>
<td>15 on Mar. 22</td>
<td>Egress and predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>24 on Nov. 21</td>
<td>17 on Mar. 31</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>47 on Dec. 5</td>
<td>23 on Mar. 18</td>
<td>Largely egress</td>
</tr>
</tbody>
</table>

Territory number 4 (table 4) was adjacent to territories number 17, number 18 and number 19; and, taken for the four territories collectively, the survival figures show a much greater uniformity than for any territory individually, as will be demonstrated later (table 22).

TABLE 5. TERRITORY NO. 5 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>31 on Dec. 1</td>
<td>25 on Feb. 15</td>
<td>Largely egress</td>
</tr>
<tr>
<td>1930-31</td>
<td>48 on Dec. 21</td>
<td>47 on Mar. 14</td>
<td>Predation</td>
</tr>
<tr>
<td>1931-32</td>
<td>75 on Nov. 25</td>
<td>61 on Mar. 20</td>
<td>Starvation and predation</td>
</tr>
<tr>
<td>1932-33</td>
<td>125 on Dec. 12</td>
<td>111 on Mar. 28</td>
<td>Principally predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>151, mid Nov.</td>
<td>105, late Mar.</td>
<td>Principally predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>92 on Dec. 1</td>
<td>50, late Mar.</td>
<td>Mainly egress and starvation</td>
</tr>
</tbody>
</table>

Territory number 5 (table 5) is in actuality a combination of closely adjacent covey territories so overlapped and so promiscuously covered by the quail population that any attempt at further sub-division would be hopeless. The combination of territories in this instance may then be regarded as an environmental unit, differing from a circumscribed individual territory only in scale.

During the first two winters of the researches, the territory was not filled up to anywhere near its capacity, since the bobwhite population had not completed its recovery from the terrific starvation mortality which it was known to have suffered during the winter of 1928-29. Nor had full recovery evidently been completed by 1931-32, though for the Prairie du Sac areas as a whole the population had at this time ascended past carrying capacity [Errington (26)]. A minor amount of starvation took place in 1931-32, probably enough to contribute decidedly to the rather high proportion of birds lost for the population level indicated.

CWA roadside debrushing activities of 1933-34 may have lowered the carrying capacity of the combined territories for that season. In 1934-35, for a population probably below carrying capacity, the predation loss was rather immaterial, but the loss from storm and egress was high.

The data from territory number 6 (table 6) lose a great deal of their heterogeneous aspect when considered jointly with
TABLE 6. TERRITORY NO. 6—PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>26 on Dec. 1</td>
<td>24 on Feb. 15</td>
<td>Predation</td>
</tr>
<tr>
<td>1930-31</td>
<td>31 on Dec. 22</td>
<td>34 on Feb. 1</td>
<td>Infusion: later lost</td>
</tr>
<tr>
<td>1931-32</td>
<td>20 on Dec. 1</td>
<td>18 on Mar. 17</td>
<td>Infusion of 4; loss of 6 atypical</td>
</tr>
<tr>
<td>1932-33</td>
<td>33 on Nov. 26</td>
<td>29 on Mar. 21</td>
<td>Predation and traffic</td>
</tr>
<tr>
<td>1933-34</td>
<td>33 on Nov. 13</td>
<td>25 on Mar. 22</td>
<td>Predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>14 on Nov. 10</td>
<td>0 by Dec. 17</td>
<td>Mainly egress to No. 53</td>
</tr>
</tbody>
</table>

the data from adjacent territories. For example, the low survival for 1931-32 is easily explained by the fact that the occupancy of another territory (number 54) (table 58) brought about a condition of over-crowding on a comparatively small area of common range; the combined survival for territories number 6 and number 54 (actually inclusive with number 6) was 37 instead of the 18 for number 6 alone.

If territory number 6 is considered as a larger unit, embracing all occupied quail land occurring as a semi-isolated block, between which and neighboring territories a surprisingly small amount of winter interchange has been detected, we may recast the data in a more intelligible way: (table 7).

TABLE 7. TERRITORY NO. 6 AND ASSOCIATED TERRITORIES (No. 12, No. 15, No. 16, and No. 54).

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>37 on Dec. 3</td>
<td>24 on Feb. 16</td>
<td>Egress; little predation</td>
</tr>
<tr>
<td>1930-31</td>
<td>62 on Dec. 21</td>
<td>62 on Feb. 1</td>
<td>No loss; predation later</td>
</tr>
<tr>
<td>1931-32</td>
<td>60 by Dec.</td>
<td>46 on Mar. 15</td>
<td>Miscellaneous mortality</td>
</tr>
<tr>
<td>1932-33</td>
<td>65 on Dec. 9</td>
<td>53 on Mar. 21</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>106 on Nov. 21</td>
<td>66 on Mar. 22</td>
<td>Predation and egress</td>
</tr>
<tr>
<td>1934-35</td>
<td>72 on Dec. 1</td>
<td>50 on Mar. 18</td>
<td>Predation; interchange</td>
</tr>
</tbody>
</table>

The population of territory number 6 and associated territories (table 7) for 1929-30 was distinctly below the carrying capacity of the land, not having recovered from the starvation losses of 1928-29. A small covey, finding an outside territory partially occupied and attractive, had left by mid-winter. One or two birds were killed by predators.

The 62 birds counted on Feb. 1, 1931, represent a too high survival figure for the season, as a subsequent loss of at least 4 from predation was known to have taken place. For the season of 1931-32, a mortality of at least 6 should be charged to poaching and accident. The losses for 1932-33 and 1933-34 may be attributable largely to predation, although 10 of the 40 birds missing for 1933-34 apparently had moved out.

Leaving out the survival for the under-populated season of 1929-30, and making as correct allowances as we can for the unrecorded late season predation of 1930-31 and the atypical accident and shooting mortality of 1931-32, we would get more nearly normal survival figures of 58-52-53-66-50, for the five
winters from 1930 to 1935. The 1933-34 population was plainly top heavy and doubtless continued to suffer loss at a high rate for some time after March 22.

TABLE 8. TERRITORY NO. 7—AMES, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>57 on Dec. 17</td>
<td>51 on Mar. 19</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>42 on Dec. 13</td>
<td>38 on Feb. 27</td>
<td>Predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>53 on Nov. 27</td>
<td>0 on Jan. 24</td>
<td>Eviction</td>
</tr>
</tbody>
</table>

Considerable debrushing of territory number 7 (table 8) had occurred during the seasons of 1932-33 and 1933-34, but we rather doubt now that the carrying capacity was affected to any pronounced degree. In the season of 1934-35, however, fall plowing of an entire large corn field, upon which the quail population of the territory depended for food, resulted in a wholesale though not simultaneous eviction. The largest covey of 31 left first; by Jan. 15 but 4 remained. Except for this eviction, the survival probably would have been in the vicinity of 48, judging from the past records of wintering populations.

TABLE 9. TERRITORY NO. 8—AMES, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>23 on Dec. 17</td>
<td>20 on Mar. 20</td>
<td>Egress</td>
</tr>
<tr>
<td>1933-34</td>
<td>23 on Jan. 13</td>
<td>21 ? on Feb. 27</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>22 on Nov. 22</td>
<td>7 on Mar. 1</td>
<td>Egress; some predation</td>
</tr>
</tbody>
</table>

We are not at all sure as to just what happened in territory number 8 (table 9) during the season of 1934-35 [Errington (32)]. The continued disappearance of one well situated resident covey after another in this general area without evidence of mortality suggests trapping operations, but of this we have no definite proof. Indeed, number 8 was the only territory in one and a half square miles that succeeded in holding any quail at all, on a tract that in 1932-33 had wintered 96 birds in 7 coveys.

TABLE 10. TERRITORY NO. 9—FT. DES MOINES, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>20 ? on Dec. 18</td>
<td>20 on Mar. 20</td>
<td>Loss of 1 from predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>20 on Dec. 11</td>
<td>20 on Jan. 8</td>
<td>Egress of 12 by Feb. 27</td>
</tr>
<tr>
<td>1934-35</td>
<td>26 ? by late Dec.</td>
<td>24 on Feb. 8</td>
<td>Predation</td>
</tr>
</tbody>
</table>

The territories surrounding number 9 (table 10), on an observational area of about a square mile, were commonly not occupied for the entire winter.
TABLE 11. TERRITORY NO. 10—DES MOINES, IOWA. CITY WATER-WORKS SUPPLY GROUNDS (WILD LIFE REFUGE).

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>59 on Dec. 16</td>
<td>55 on Feb. 8</td>
<td>Predation and egress</td>
</tr>
<tr>
<td>1933-34</td>
<td>59 on Dec. 8</td>
<td>54 on Feb. 27</td>
<td>Predation and egress</td>
</tr>
<tr>
<td>1934-35</td>
<td>14 on Nov. 23</td>
<td>33 on Mar. 1</td>
<td>Influx</td>
</tr>
</tbody>
</table>

The higher wintering densities of the first two seasons on territory number 10 (table 11) were due almost entirely to the excellence of the feeding program carried on by the City Waterworks employees. During the past season, at our request, the feeding program on the sample tract under observation was experimentally delayed and restricted, with a resultant lowering of the wintering bob-white population. The heavy influx evident by March 1 may be attributed to the resumption of the feeding operations and to food shortage on private lands adjacent to the area.

SURVIVAL DATA—SECOND CLASS

(Data differing from those of Class One in that they were secured from territories not so likely to hold quail year after year; the territories were, however, similarly bounded by barriers or by territories under contemporaneous observation, and the data were similarly uncomplicated by starvation or by atypical losses.)

TABLE 12. TERRITORY NO. 11—PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>22 on Jan. 4</td>
<td>30 on Mar. 29</td>
<td>Influx of 8 in early January</td>
</tr>
<tr>
<td>1930-31</td>
<td>Territory not occupied.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>32 on Dec. 18</td>
<td>32 on Mar. 23</td>
<td>No loss</td>
</tr>
<tr>
<td>1932-33</td>
<td>Territory not occupied; birds evicted by the burning of a strategically located brush pile.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>14 on Nov. 14</td>
<td>19 on Mar. 22</td>
<td>Influx; some egress</td>
</tr>
<tr>
<td>1934-35</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Territory number 11 (table 12) was a farmyard territory offering a secure habitat as long as the birds could range between a corncrib and a huge brush pile nearby. With the burning of the brush pile, the territory lost its attractiveness, if not much of its habitability. During 1934-35 a different part of the territory was occupied by 10 of the birds; 9 used the old range.

TABLE 13. TERRITORY NO. 12—PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>11 on Jan. 3</td>
<td>16 on Feb. 1</td>
<td>Egress</td>
</tr>
<tr>
<td>1930-31</td>
<td>15 on Dec. 22</td>
<td>0 on Feb. 16</td>
<td>Influx</td>
</tr>
<tr>
<td>1931-32</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>19 on Nov. 17</td>
<td>13 on Mar. 28</td>
<td>Egress and predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>9 on Jan. 5</td>
<td>11 on Mar. 31</td>
<td>Influx</td>
</tr>
<tr>
<td>1934-35</td>
<td>12 on Dec. 1</td>
<td>0 by Jan. 7</td>
<td>Mainly predation</td>
</tr>
</tbody>
</table>
Territory number 12 (table 13) is on the border line of habitability and attractiveness and is situated between other territories which are more desirable to wintering bob-whites, though occasionally subject to over-crowding. As a consequence, territory number 12 is the scene of endless shifting and some mortality. Birds come and go, and sometimes, as in 1931-32 when an excessive amount of fencerow debrushing took place, the territory may not be occupied. In 1934-35, the vulnerability of the resident covey may have been increased by the temporary massing of a combined covey of 26 nearby [Errington (32)]. The territory is one of the number 6 group, and its populations are apparently influenced by densities of neighboring coveys.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>8 on Jan. 4</td>
<td>0 before Feb. 15</td>
<td>Egress into better territory</td>
</tr>
<tr>
<td>1930-31</td>
<td>10 on Dec. 21</td>
<td>11 on Feb. 9</td>
<td>Influx; no mortality</td>
</tr>
<tr>
<td>1931-32</td>
<td>13 on Oct. 21</td>
<td>0 by Nov. 7</td>
<td>Egress to adjacent territory</td>
</tr>
<tr>
<td>1932-33</td>
<td>Territory vacant during winter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>18 on Oct. 14</td>
<td>Winter fluctuation between 8 and 12</td>
<td></td>
</tr>
<tr>
<td>1934-35</td>
<td>15 on Dec. 24</td>
<td>4 on Mar. 1</td>
<td>Probably predation</td>
</tr>
</tbody>
</table>

Territory number 13 (table 14) is the sort of territory that may or may not remain occupied, depending largely upon the attractiveness of adjacent territories. In common with the territory number 12, it was essentially occupiable (except for the last season), however, in contrast with the lethal territory number 14 (table 15). Roadside debrushing at a strategic place near a farmyard in 1933-34 probably made the territory lethal for the following winter, when birds were forced into the farmyard to feed.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>8 on Jan. 3</td>
<td>0 by Mid-Jan.</td>
<td>Egress</td>
</tr>
<tr>
<td>1930-31</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>23 on Jan. 10</td>
<td>2 on Mar. 23</td>
<td>Predation</td>
</tr>
<tr>
<td>1932-33</td>
<td>12 on Nov. 26</td>
<td>0 by Jan. 3</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>24 on Oct. 31</td>
<td>0 by Mar. 22</td>
<td>Largely predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>17 on Nov. 24</td>
<td>0 by Feb. 21</td>
<td>Egress and unknown</td>
</tr>
</tbody>
</table>

The lethal territory number 14 (table 15) is the best example of its kind that we have of environment incapable of wintering quail, yet inviting enough to attract unfavorably situated birds to their almost certain doom. The deficiency seems to be one of cover; and while the major proportion of the mortality suffered may be traced to predation, the kinds and numbers of predators have apparently had little influence. The coveys occupying this territory are evidently vulnerable to predation by reason of
their insecurity of position. Few predators or many predators, the territory in its present state is not habitable for bob-whites in winter.

TABLE 16. TERRITORY NO. 15 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>16 on Dec. 22</td>
<td>12 on Feb. 1</td>
<td>Egress</td>
</tr>
<tr>
<td>1931-32</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>16 on Nov. 21</td>
<td>16 on Mar. 31</td>
<td>Loss of 8 newcomers from predation. See text</td>
</tr>
<tr>
<td>1934-35</td>
<td>16 on Nov. 10</td>
<td>12 on Mar. 18</td>
<td>Egress to No. 19</td>
</tr>
</tbody>
</table>

The data for territory number 15 (table 16) for 1933-34 (recorded in the field notes but too complicated to be shown in the table) indicate that the normal carrying capacity is in the vicinity of 16 and that losses from predators occurred corresponding to the number of birds which came in to exceed that figure—8 birds influx and loss during the season. This territory and number 16 as well should be considered one of the number 6 group (table 7).

TABLE 17. TERRITORY NO. 16 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>14 on Dec. 22</td>
<td>10 on Feb. 1</td>
<td>Predation</td>
</tr>
<tr>
<td>1931-32</td>
<td>14 on Dec. 9</td>
<td>9 on Mar. 16</td>
<td>Predation</td>
</tr>
<tr>
<td>1932-33</td>
<td>13 on Dec. 9</td>
<td>11 on Apr. 1</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>12 on Dec. 6</td>
<td>0 by Feb. 10</td>
<td>Probable egress</td>
</tr>
<tr>
<td>1934-35</td>
<td>17 on Dec. 1</td>
<td>10 on Feb. 12</td>
<td>Probable predation</td>
</tr>
</tbody>
</table>

Territory number 16 (table 17) was not occupied during the season of 1929-30 because the population had not recovered sufficiently from the 1928-29 starvation mortality to fill it up. In 1933-34, the covey of 12 seemed to have moved out by Feb. 10 of its own volition; it was not known to have suffered mortality prior to its egress. In 1934-35, there was much shifting and temporary invasion by outside birds [Errington (32)].

TABLE 18. TERRITORY NO. 17 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>20 on Dec. 22</td>
<td>20 on Mar. 30</td>
<td>No loss</td>
</tr>
<tr>
<td>1931-32</td>
<td>33 Mid-Dec.</td>
<td>33 on Mar. 23</td>
<td>No loss</td>
</tr>
<tr>
<td>1932-33</td>
<td>23 on Dec. 20</td>
<td>24 on Mar. 22</td>
<td>Influx 2; mortality of 1</td>
</tr>
<tr>
<td>1933-34</td>
<td>19 on Dec. 10</td>
<td>14 on Mar. 31</td>
<td>Predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>10 on Dec. 3</td>
<td>11 on Mar. 25</td>
<td>Influx</td>
</tr>
</tbody>
</table>

As was the case for territory number 16, territory number 17 (table 18) was unoccupied during 1929-30, the first season after the catastrophic winter of 1928-29. Thereafter it was occupied,
but at first glance one may suspect not up to full carrying capacity, as only a single bird was lost from predation in the following three winters. (The data should be considered not from territory number 17 alone but collectively from the combined adjacent territories of number 4, number 17, number 18 and number 19—see table 22.) Then, by Dec. 18, 1933, the CWA roadside debrushing crews had destroyed the principal cover in the territory and had thus forced the resident covey into a precarious existence during which the birds found their chief refuge in a farmyard, in a cement culvert, and in the open weedy and stubble growths of fields. In 1934-35, the territory was occasionally visited by birds from the now over-populated number 4.

### TABLE 19. TERRITORY NO. 18 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>20 on Dec. 18</td>
<td>16 on Mar. 17</td>
<td>Predation</td>
</tr>
<tr>
<td>1932-33</td>
<td>27 on Nov. 9</td>
<td>20 on Apr. 1</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>25 on Jan. 9</td>
<td>20 on Mar. 19</td>
<td>Predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>14 on Jan. 10</td>
<td>0 by Jan. 30</td>
<td></td>
</tr>
</tbody>
</table>

### TABLE 20. TERRITORY NO. 19 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>24 on Dec. 22</td>
<td>20 on Feb. 1</td>
<td>Predation</td>
</tr>
<tr>
<td>1931-32</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>22 on Dec. 8</td>
<td>0 by Mid. Jan.</td>
<td>Mainly egress into number 18</td>
</tr>
<tr>
<td>1934-35</td>
<td>20 ? by Dec.</td>
<td>25 by Mar. 18</td>
<td>Influx from number 15</td>
</tr>
</tbody>
</table>

Territories number 18 and number 19 (tables 19 and 20), while distinct, are adjacent and may be considered more advantageously as common ground for the coveys resident: (table 21).

### TABLE 21. COMBINATION OF TERRITORIES NO. 18 AND NO. 19.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>24 on Dec. 22</td>
<td>20 on Feb. 1</td>
<td>Predation</td>
</tr>
<tr>
<td>1931-32</td>
<td>20 on Dec. 18</td>
<td>16 on Mar. 17</td>
<td>Predation</td>
</tr>
<tr>
<td>1932-33</td>
<td>27 on Nov. 9</td>
<td>20 on Apr. 1</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>25 on Jan. 7</td>
<td>20 on Mar. 19</td>
<td>Predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>34 in Dec.</td>
<td>25 by Mar. 18</td>
<td>Egress; some influx</td>
</tr>
</tbody>
</table>

In combination, then, territories number 18 and number 19 (table 21) present more of a unified picture of winter bobwhite survival than either one alone. Combined with the adjacent territories number 4 and number 17 of the same natural group, they present a picture still more unified and one
that reveals a surprising definiteness of year to year carrying capacity, not so much for an individual territory but for the group of territories constituting the common range of the resident winter population: (table 22).

### Table 22. Combination of Territories No. 4, No. 17, No. 18 and No. 19.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>15 on Jan. 4</td>
<td>14 on Feb. 15</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1930-31</td>
<td>64 on Dec. 22</td>
<td>60 by Mar.</td>
<td>Predation</td>
</tr>
<tr>
<td>1931-32</td>
<td>72 by Dec.</td>
<td>64 by Mar.</td>
<td>Predation</td>
</tr>
<tr>
<td>1932-33</td>
<td>68 by Dec.</td>
<td>59 by late Mar.</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>68 by Dec.</td>
<td>51 by late Mar.</td>
<td>Predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>91 by Dec.</td>
<td>59 by late Mar.</td>
<td>Predation and egress</td>
</tr>
</tbody>
</table>

The tract of land making up the combined covey territories number 4, number 17, number 18 and number 19 (table 22) was, of course, under-populated in 1929-30, the first season following the starvation mortality of 1928-29; in fact, territory number 4 was the only one of this group to have a wintering covey for that season. Survivals for the next three winters showed a fair degree of constancy, namely 60, 64 and 59. The lower survival of 51 for 1933-34 is entirely to be expected in view of the wholesale removal of brushy vegetation along the roadsides in connection with CWA unemployment relief activities. In 1934-35, the survival was probably somewhat higher than it would have been except that one of the principal coveys was situated near territory number 15, which it partially shared to convenient advantage.

### Table 23. Territory No. 20 — Prairie du Sac, Wis.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>25 on Jan. 10</td>
<td>21 on Mar. 19</td>
<td>Predation</td>
</tr>
<tr>
<td>1932-33</td>
<td>28 on Dec. 12</td>
<td>22 on Mar. 23</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>Territory not regularly occupied</td>
<td></td>
<td>Egress to number 13</td>
</tr>
<tr>
<td>1934-35</td>
<td>18 on Nov. 14</td>
<td>0 by Dec. 24</td>
<td></td>
</tr>
</tbody>
</table>

Although territory number 20 (table 23) is not a choice territory, the survival of 21 for the season of 1931-32 and of 22 for 1932-33 hints a substantial carrying capacity for favorable years. During 1933-34, the territory was not occupied by a truly resident population but was split into a number of partial covey ranges. In 1934-35, the food supply was too short to hold the birds later than December. They then moved to a portion of territory number 13 (table 14) which proved to be lethal for the season.

### Table 24. Territory No. 21 — Ft. Des Moines, Iowa.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>11 ? on Dec. 18</td>
<td>5 on Mar. 5</td>
<td>Egress</td>
</tr>
<tr>
<td>1933-34</td>
<td>5 on Jan. 8</td>
<td>5 on Feb. 27</td>
<td>No loss</td>
</tr>
<tr>
<td>1934-35</td>
<td>4 on Jan. 4</td>
<td>15 on Feb. 8</td>
<td>Influx</td>
</tr>
</tbody>
</table>
Territory number 21 (table 24) may perhaps be only a part of a larger territory, but it seems to show sufficient identity of its own to be considered separately. The heavy survival figure of 1934-35 was due mostly to a strong late influx.

**TABLE 25. TERRITORY NO. 22 — FT. DES MOINES, IOWA.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1933-34</td>
<td>15 ? Dec. 11</td>
<td>17 on Feb. 27</td>
<td>?</td>
</tr>
<tr>
<td>1934-35</td>
<td>16 ? Jan. 4</td>
<td>15 on Feb. 8</td>
<td>Predation</td>
</tr>
</tbody>
</table>

**TABLE 26. TERRITORY NO. 23 — DES MOINES, IOWA, WATERWORKS SUPPLY GROUNDS (WILD LIFE REFUGE).**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>20 on Dec. 16</td>
<td>0 by Mar. 20</td>
<td>Egress</td>
</tr>
<tr>
<td>1933-34</td>
<td>12 on Dec. 8</td>
<td>0 by Feb. 27</td>
<td>Egress</td>
</tr>
<tr>
<td>1934-35</td>
<td>19 on Nov. 23</td>
<td>0 by Feb. 9</td>
<td>Egress</td>
</tr>
</tbody>
</table>

Territory number 23 (table 26) was attractive enough to hold quail only during the first half of winter; thereafter, the birds shifted to more favored adjacent territories (for example, number 10), even though they were well situated and relatively undisturbed. There was nothing perceptibly wrong with the territory, yet the birds left. Possibly number 23 may be more correctly thought of as a part of number 10 and number 24.

**TABLE 27. TERRITORY NO. 24 — DES MOINES, IOWA, WATERWORKS SUPPLY GROUNDS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>18 on Jan. 12</td>
<td>14 by Feb. 27</td>
<td>Mainly egress</td>
</tr>
<tr>
<td>1933-34</td>
<td>12 on Nov. 23</td>
<td>0 by Dec. 4</td>
<td>Egress; no food</td>
</tr>
</tbody>
</table>

Territory number 24 (table 27) is not habitable under present conditions without winter feeding. In 1933-34, the establishment of feeding stations resulted in the secure accommodation of a covey of quail. The feeding was not continued the following season, and the covey present in early winter soon had to leave.

**TABLE 28. TERRITORY NO. 25 — AMES, IOWA.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>20 on Dec. 14</td>
<td>0 by Feb. 12</td>
<td>Largely egress</td>
</tr>
<tr>
<td>1933-34</td>
<td>15 on Jan. 14</td>
<td>0 by late Jan.</td>
<td>Egress</td>
</tr>
<tr>
<td>1934-35</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Territory number 25 (table 28) is plainly not choice environment. The departure of the occupying coveys for 1932-33 and 1933-34 may signify lack of habitability. That it was not occupied in 1934-35 may not be so significant, as the quail population was too low that season to fill up territories of known superior quality.
### TABLE 29. TERRITORY NO. 26 — AMES, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>38 on Nov. 25</td>
<td>36 on Mar. 22</td>
<td>Possibly predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>30 on Jan. 16</td>
<td>0 by Feb. 27</td>
<td>Apparently egress</td>
</tr>
<tr>
<td>1934-35</td>
<td>26 on Dec. 14</td>
<td>2 by Mar. 9</td>
<td>Apparently egress</td>
</tr>
</tbody>
</table>

In 1933-34, the apparent egress from territory number 26 (table 29) seemed at least partly compensated by an influx into territory number 28 (table 31). We don’t know what happened in 1934-35, but we are very sure that the losses from predation were light; birds seemed merely to disappear, usually in small groups (egress of 10 of the last 12 birds was rather definitely traced, however). [Errington (32)].

### TABLE 30. TERRITORY NO. 27 — AMES, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>11 on Nov. 26</td>
<td>11 on Mar. 21</td>
<td>No loss</td>
</tr>
<tr>
<td>1933-34</td>
<td>14 on Jan. 18</td>
<td>0 by Feb. 27</td>
<td>Apparently egress</td>
</tr>
<tr>
<td>1934-35</td>
<td>11 on Nov. 22</td>
<td>5 by Jan. 23</td>
<td>Unknown</td>
</tr>
</tbody>
</table>

The shrinkage of the covey occupying territory number 27 (table 30) in 1934-35 was gradual and exceedingly baffling. Despite very careful search no sign of mortality could be found. The territory was situated in close proximity to a settlement of squatter’s shacks, and some losses may have been due to poaching by the hunters who were constantly in evidence.

### TABLE 31. TERRITORY NO. 28 — AMES, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>14 on Jan. 7</td>
<td>13 on Mar. 20</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>38 on Jan. 14</td>
<td>31 ? on Feb. 27</td>
<td>Some predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>15 on Nov. 24</td>
<td>Birds did not stay</td>
<td></td>
</tr>
</tbody>
</table>

The population of number 28 (table 31) for 1933-34 appeared to be partly composed of birds also ranging in territories number 25 and number 26. This season, the food supply was much superior to that of the surrounding territories, and resulted in an exceptional concentration of birds during the greater part of the winter. Whether the subsequent egress of the birds of number 26 had any relation to the concentration at number 28 is hard to say. For all of the territories number 25 to number 28, the data may be said to be generally inadequate to justify any conclusions as to carrying capacity.

**SURVIVAL DATA—THIRD CLASS**

(Data differ from those of Classes One and Two chiefly in that emergency starvation losses complicated efforts to determine carrying capacities of the respective territories; these territories of Class Three were similarly bounded by barriers or by territories kept under contemporaneous observation, as were the territories of Classes One and Two.)
TABLE 32. TERRITORY NO. 29 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>16 on Dec. 23</td>
<td>13 on Feb. 28</td>
<td>Predation; 1 collected</td>
</tr>
<tr>
<td>1931-32</td>
<td>24 on Nov. 16</td>
<td>12 on Apr. 6</td>
<td>Egress; predation and starvation</td>
</tr>
<tr>
<td>1932-33</td>
<td>22 on Dec. 18</td>
<td>17 on Mar. 23</td>
<td>Predation and food shortage</td>
</tr>
<tr>
<td>1933-34</td>
<td>11 on Oct. 23</td>
<td>8 on Feb. 27</td>
<td>Predation and food shortage</td>
</tr>
<tr>
<td>1934-35</td>
<td>27 on Nov. 14</td>
<td>16 on Mar. 22</td>
<td>Probably predation</td>
</tr>
</tbody>
</table>

The 1930-31 survival of territory number 29 (table 32) should have been 14, as one bird was collected late for examination. The survival for 1931-32 was doubtless somewhat below normal by reason of the loss of a few birds from late winter starvation (from Jan. 16 until March the population had been 18 birds). The 1933-34 covey of 11 lost no birds until the food situation became acute about mid-February, which indicates an intrinsic security of population from predation at this level.

Taking into account the losses occasioned by late winter starvation and the apparent vulnerability to, and the security from, predation of the wintering birds at different population levels, we may then say that the normal carrying capacity for territory number 29 seems to be between 14 and 17, probably nearer the latter number.

TABLE 33. TERRITORY NO. 30 — PINE BLUFF, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>18 on Jan. 25</td>
<td>5 by Mar. 3</td>
<td>Starvation</td>
</tr>
<tr>
<td>1930-31</td>
<td>Territory unoccupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>10 on Jan. 5</td>
<td>16 on Mar. 22</td>
<td>See text</td>
</tr>
</tbody>
</table>

The data from territory number 30 (table 33) are too heterogeneous to be expressed well in tabular form, although they are of reliable quality. The territory is sufficiently marginal to be subject to unpredictable influx, egress and emergency losses; yet under open winter conditions, it seemed to have a carrying capacity of about 16 birds for the two seasons occupied.

In 1929-30, the loss of 13 out of 18 was practically all due to starvation (except for two birds killed by predators). A subsequent March influx of 18 from the adjacent fortuitous territory number 61 (see table 65 and discussion), after food had been made available through melting of the snow, was fairly well accommodated. Territory number 30 was not completely abandoned in 1930-31, but was visited only occasionally by a covey from number 34.

The history of the wintering population for 1931-32 is rather
involved. By Jan. 30, a covey of 20 had joined the 10 already resident, to depart for the emergency territory number 58 by Feb. 3. The covey of 10 had also gone to number 58 by March 2. By March 15, the 19 survivors in territory number 58 had returned to number 30, where they were still insecure enough to lose 3 more from predation by March 22.

**TABLE 34. TERRITORY NO. 31 — HONEY CREEK BOTTOMS, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>17 on Jan. 4</td>
<td>12 on Feb. 16</td>
<td>Starvation</td>
</tr>
<tr>
<td>1930-31</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>16 on Dec. 7</td>
<td>13 on Mar. 23</td>
<td>Apparently storm</td>
</tr>
</tbody>
</table>

**TABLE 35. TERRITORY NO. 32 — HONEY CREEK BOTTOMS, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>20 on Jan. 4</td>
<td>0 by Feb. 16</td>
<td>Starvation</td>
</tr>
<tr>
<td>1930-31</td>
<td>23 on Nov. 25</td>
<td>19 by Feb. 9</td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>20 on Dec. 3</td>
<td>0 on Mar. 23</td>
<td>Egress</td>
</tr>
</tbody>
</table>

The adjacent territories number 31 and number 32 (tables 34 and 35) were commonly too deficient in food to be regularly habitable during periods of snow. During open winter weather, the birds were securely situated, so far as predators were concerned; and the carrying capacities for the territories were probably not far from the number usually beginning the winter, or about 16 for number 31 and about 20 for number 32.

**TABLE 36. TERRITORY NO. 33 — PINE BLUFF, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>25 on Jan. 23</td>
<td>11 on Feb. 12</td>
<td>Mainly starvation</td>
</tr>
<tr>
<td>1930-31</td>
<td>13 on Dec. 20</td>
<td>11 on Feb. 12</td>
<td>Predation</td>
</tr>
<tr>
<td>1931-32</td>
<td>20 on Jan. 4</td>
<td>12 on Mar. 4</td>
<td>Unknown</td>
</tr>
</tbody>
</table>

The territory number 33 (table 36) survival of 11 for 1929-30, compared with the 11 and 12 survivals for the next two seasons, may not have the significance apparent at first glance, because of the probable role of emergency losses reducing the population to this level. This territory seems to be somewhat submarginal in quality or at least in attractiveness, for the surviving populations in all three instances moved out toward the end of the winter after the dates given in the table. Territory number 33 belongs in about the same category as number 30, subject to the same likelihood of sudden influx, egress, or emergency mortality, but it probably has a carrying capacity not far from the 11 or 12 indicated.

**TABLE 37. TERRITORY NO. 34 — PINE BLUFF, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>21 on Dec. 20</td>
<td>21 on Feb. 8</td>
<td>No loss; see text</td>
</tr>
<tr>
<td>1931-32</td>
<td>18 on Jan. 27</td>
<td>10 on Mar. 22</td>
<td>Starvation</td>
</tr>
</tbody>
</table>
The primary weakness of territory number 34 (table 37) is that, while there is a food supply sufficient for open winters (as 1930-31), it is unavailable during periods of heavy snow. During the first season (1929-30), the covey which should logically have occupied this territory stationed itself in a territory (number 61) used only the one season, but made temporarily attractive by a farmer spreading grain-bearing manure in the fields; toward the end of the winter it moved in to repopulate the starvation-depleted territory number 30.

For 1930-31, there was no starvation loss for the sole reason that not enough snow fell, or remained, to keep the food on the ground covered; in 1931-32, a comparatively brief period of crisis was attended by wholly expected mortality. For open winters, the carrying capacity of the territory seems to be in the vicinity of 20 birds.

SURVIVAL DATA—FOURTH CLASS

(Data reliable as to accuracy of counts unless otherwise indicated but of less reliability than Classes One to Three because of the nearness of uncensused coveys to those under regular observation; data may also be complicated by starvation emergencies but are commonly not. In short, the territories in this class are those located at the edges of observational areas.)

| TABLE 38. TERRITORY NO. 35 — PRAIRIE DU SAC, WIS. |
|---|---|---|---|
| Season | First count | Final count | Cause of difference |
| 1929-30 | Territory not occupied | | |
| 1930-31 | 7 on Dec. 23 | 7 ? on Mar. 30 | No apparent loss |
| 1931-32 | 15 on Dec. 3 | 16 on Feb. 16 | See Text |
| 1932-33 | 21 on Dec. 2 | 19 on Mar. 22 | See Text |
| 1933-34 | 5 on Dec. 23 | 4 ? on Jan. 18 | See Text |
| 1934-35 | 14 on Dec. 7 | 14 on Mar. 22 | See Text |

During the seasons of 1931-32, 1932-33 and 1934-35, territory number 35 (table 38) was the partial range of an uncensused covey just outside of the observational area. Interchange occurred at times but to what extent is unknown. For the season of 1933-34, the territory seemed to be left largely to the small covey of 5, the survivors of which left the territory in late January.

| TABLE 39. TERRITORY NO. 36 — NAKOMA, WIS. |
|---|---|---|---|
| Season | First count | Final count | Cause of difference |
| 1929-30 | 8 on Nov. 4 | 0 by Dec. 1 | Egress |
| 1930-31 | About 15 during winter (Dickson) | | |
| 1931-32 | About 18 during winter (Dickson) | | |
| 1932-33 | 8 on Feb. 3 | 10 by Mar. 29 | Influx |
| 1933-34 | About 10 during winter (Dickson) | | |
| 1934-35 | About 15 during winter (Dickson) | | |

In contrast with the situation in many of the Prairie du Sac territories, there was no evident under-population of bob-
whites in the Nakoma-Wingra Refuge area during the winter of 1929-30. Birds were in the vicinity but apparently did not find territory number 36 (table 39) wholly to their liking.

Territory number 36 owes whatever habitability and attractiveness it has largely to a supply of corn and barley which is kept beside a marsh for the feeding of a population of semi-domesticated wild mallard ducks. Both quail and ducks have used one main heap of piled grain as a common feeding place. A variable number of pheasants also have used the grain pile.

It may be no more than coincidence that the quail used this territory in the smallest numbers during two seasons (1929-30 and 1933-34) when the wintering flock of ducks was the largest. Table 40 is based upon the combined notes of Errington and Dr. J. G. Dickson (University of Wisconsin).

| TABLE 40. TERRITORY NO. 36 — NAKOMA, WIS. |
|-----------------|-----------------|-----------------|
| 1929-30         | 100             | 6               | 0 except early      |
| 1930-31         | 65              | 10              | 15                 |
| 1931-32         | 85              | 15              | 18                 |
| 1932-33         | 70              | 12              | 8 to 10            |
| 1933-34         | 115             | 15              | 10                 |
| 1934-35         | 35              | 20              | 15                 |

The numbers given for mallards and pheasants are approximate rather than exact, but they are considered quite reliable; the numbers for quail less reliable, except those from 1929-30 and 1932-33. Altogether, we are not at all sure that these limited data have any real territorial significance. They seem to hint faintly that quail may tend to avoid mounting numbers of conspicuous birds or that their own security may be lessened by concentrations of conspicuous species occupying the same range.

The above may appear to be just another expression of the commonly held ideas relative to the effect of heavy densities of "buffer" species attracting predators, with consequent losses to quail. We do not believe, however, that the explanation (if there is one, or if there is anything to explain) is as simple as that. The influence of "buffer" populations on winter quail losses from predation seems not too clear [see Errington (26) and discussion later in this bulletin].

| TABLE 41. TERRITORY NO. 37 — UNIVERSITY HILL FARM, MADISON, WIS. |
|-----------------|-----------------|-----------------|
| Season          | First count     | Final count     | Cause of difference |
| 1929-30         | 13 on Nov. 5    | 20 on Mar. 2    | Influx               |
| 1930-31         | 25 on Jan. 6    | 28 on Mar. 17   | Influx from No. 3    |
| 1931-32         | 35 on Dec. 9    | 0 by Jan. 3     | Eviction by pheasants|
| 1932-33         | Territory not occupied | | |
By March 23, 13 of the 1929-30 population of territory number 37 (table 41) had moved to the lately vacant territory number 3 (table 3). The territory was not occupied during the season of 1932-33 because of food shortage due to agricultural practices.

The evident abandonment of the territory to ring-necked pheasants in 1931-32 is significant. Most of the pheasants in the entire University Hill Farm area were localized about territory number 37, but not until 1931-32 did they congregate in sufficient densities to bring about a recognized eviction of the quail [Errington (20)]. The quail simply seemed to leave when the pheasants became too numerous; no actual strife between the two species was noted.

### TABLE 42. TERRITORY NO. 38 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1931-32</td>
<td>23 on Jan. 8</td>
<td>21 on Mar. 11</td>
<td>Predation</td>
</tr>
<tr>
<td>1932-33</td>
<td>49 on Dec. 16</td>
<td>44 on Mar. 25</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>25 on Jan. 5</td>
<td>21 on Mar. 15</td>
<td>Predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>27 on Nov. 20</td>
<td>0 by Mar. 25</td>
<td>Mainly blizzard mortality</td>
</tr>
</tbody>
</table>

The uniformity of survivals for 1931-32 and 1933-34 may indicate that 21 is not far from the real carrying capacity of territory number 38 (table 42). In 1934-35, the survival by Feb. 9 was 21; then a severe blizzard apparently wiped out the whole population. The higher survival for 1932-33 may point to the presence of an unobserved territory immediately outside of territory number 38, which in combination with number 38 may be able to accommodate a greater number of birds than number 38 alone. Were this latter the case, then it would not be beyond reason to postulate that the quail population occupying the combined territories may have found it advantageous to spend the season of 1932-33 mainly in territory number 38 instead of in smaller numbers both in territory number 38 and in the adjacent but uncensused territory outside of the observational area. In that event, the situation would not differ materially from that described in connection with the combinations of territories number 6, number 54 and associated territories number 12, number 15 and number 16.

### TABLE 43. TERRITORY NO. 39 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1931-32</td>
<td>24 on Jan. 11</td>
<td>8 on Mar. 21</td>
<td>Starvation</td>
</tr>
<tr>
<td>1932-33</td>
<td>13 on Dec. 16</td>
<td>11 on Mar. 25</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>28 on Oct. 21</td>
<td>22 on Mar. 27</td>
<td>Probably mainly predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>34 on Nov. 12</td>
<td>0 by Mar. 6</td>
<td>Predation; egress starvation</td>
</tr>
</tbody>
</table>
Territory number 39 (table 43) was also located on the extreme edge of an observational area, with uncensused territories immediately beyond. During 1933-34, in particular, fluctuations in numbers of the wintering quail were noted, doubtless on account of interchange with coveys outside. There was considerable shifting in 1934-35, with as many as 42 birds present at once, but the late February blizzard brought heavy mortality and drove out those it didn’t kill.

| TABLE 44. TERRITORY NO. 40 — PINE BLUFF, WIS. |
|-----------------|-----------------|-----------------|-----------------|
| Season          | First count     | Final count     | Cause of difference |
| 1929-30         | Territory not occupied |                 |                  |
| 1931-32         | 11 on Dec. 20   | 10 on Mar. 16   | Probably predation |
| 1932-33         | 19 on Feb. 3    | 17 on Mar. 4    | Predation         |

Nothing is known of the territories adjacent to number 40 (table 44) but outside of the observational area.

| TABLE 45. TERRITORY NO. 41 — PINE BLUFF, WIS. |
|-----------------|-----------------|-----------------|-----------------|
| Season          | First count     | Final count     | Cause of difference |
| 1929-30         | o by Jan. 23    |                 | See Text         |
| 1930-31         | 25 on Dec. 20   | 23 on Mar. 16   | Predation         |
| 1931-32         | 34 on Jan. 4    | 39 on Mar. 22   | Influx 12; Predation 7 |

Territory number 41 (table 45) was first visited on Jan. 23, 1930, at which time it was ascertained that the population formerly occupying it had moved into territory number 33, there to mingle and starve with the other birds.

The population of 1930-31 may be fairly near carrying capacity, as the higher levels of 1931-32 lost at a rather high rate from predation, even before the late February or early March influx of 12 from the adjacent territory number 33.

| TABLE 46. TERRITORY NO. 42—MAZOMANIE, WIS. |
|-----------------|-----------------|-----------------|-----------------|
| Season          | First count     | Final count     | Cause of difference |
| 1930-31         | 15 on Nov. 15   | 20 on Mar. 19   | Influx; 1 collected |
| 1931-32         | 15 on Dec. 11   | 8 on Mar. 20    | Starvation; See text |

The 1931-32 population of territory number 42 (table 46) had gained 6 birds by influx by Jan. 7, and these apparently were accommodated with security until the cataclysmic starvation emergency of early March [Errington (20)].

| TABLE 47. TERRITORY NO. 43—MAZOMANIE, WIS. |
|-----------------|-----------------|-----------------|-----------------|
| Season          | First count     | Final count     | Cause of difference |
| 1931-32         | 17 on Jan. 9    | 17 on Mar. 20   | No loss          |
| 1932-33         | About same number — data not exact |                 |                  |
| 1933-34         | No data         |                 |                  |
| 1934-35         | 15 on Feb. 1    | 18 ? on Mar. 26 | Influx of about 5 by Feb. 5 |
The 1934-35 figures for territory number 43 (table 47) were contributed by Arthur Hawkins who had been carrying on survival studies of bob-white populations on several southern and central Wisconsin observational areas, under direction of Prof. Aldo Leopold of the University of Wisconsin. It so happened that Mr. Hawkins had 1934-35 data on this territory which had been formerly studied by Errington.

**TABLE 48. TERRITORY NO. 44—UNIVERSITY HILL FARM, MADISON, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>10 on Dec. 20</td>
<td>0 by Mar. 2</td>
<td>Egress</td>
</tr>
<tr>
<td>1930-31</td>
<td>Territory not occupied</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>10 on Jan. 9</td>
<td>4 on Mar. 19</td>
<td>Starvation and egress</td>
</tr>
<tr>
<td>1932-33</td>
<td>10 on Jan. 27</td>
<td>0 by Feb. 8</td>
<td>Egress (See text)</td>
</tr>
</tbody>
</table>

The 1931-32 starvation crisis for territory number 44 (table 48) arose largely as the result of competition with ring-necked pheasants for food. The egress of 1932-33 was likewise due to a food shortage caused, in this instance, by the agricultural practices discussed under territory number 3.

**TABLE 49. TERRITORY NO. 45—LAKE WINGRA, MADISON, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1930-31</td>
<td>29 on Dec. 14</td>
<td>26 on Mar. 29</td>
<td>Predation</td>
</tr>
<tr>
<td>1931-32</td>
<td>37 on Dec. 9</td>
<td>25 on Mar. 16</td>
<td>See text</td>
</tr>
</tbody>
</table>

The survivals of 26 for 1930-31 and of 25 for 1931-32 on territory number 45 (table 49) have a deceptive similarity at first glance, but in actuality most of the mortality for 1931-32 may be attributed to a March blizzard. Had it not been for this late season emergency loss, the survival for 1931-32 would probably have been in the vicinity of 35, which would indicate not definiteness of normal carrying capacity but lack thereof. It by no means follows, however, that the combination of territory number 45 and adjacent uncensused territories outside of the area might not have a more definite carrying capacity, even if number 45 alone has not. The possibility of this being true is well demonstrated by the data from territories number 4, number 17, number 18 and number 19 (table 22) when considered separately and in the aggregate.

**TABLE 50. TERRITORY NO. 46—HONEY CREEK BOTTOMS, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1930-31</td>
<td>25 on Dec. 24</td>
<td>24 on Mar. 15</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1931-32</td>
<td>35 on Dec. 3</td>
<td>18 on Mar. 23</td>
<td>Egress</td>
</tr>
</tbody>
</table>

Insofar as the coveys wintering in territory number 46 (table 50) suffered little or no loss from predation at any of the densities recorded, it is apparent that the maximum carrying capacity for the territory is near 35 birds or higher. Even the
egress of about half of the population in 1931-32 took place practically at the end of the winter and was not forced in any perceptible way. Much uncensused but occupied quail range abutted territory number 46 on three of its four sides.

**TABLE 51. TERRITORY NO. 47 — MC FARLAND, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929·30</td>
<td>27 on Dec. 7</td>
<td>19 on Mar. 24</td>
<td>Predation</td>
</tr>
<tr>
<td>1930·31</td>
<td>21 on Dec. 27</td>
<td>20 on Feb. 19</td>
<td>Probably predation</td>
</tr>
</tbody>
</table>

The presence of neighboring uncensused territories rule territory number 47 (table 51) out of Class One, but it was probably isolated enough to be entitled to consideration as a definite unit.

**TABLE 52. TERRITORY NO. 48 — MADISON, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929·30</td>
<td>33 on Dec. 17</td>
<td>31 on Feb. 7</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1930·31</td>
<td>40 on Nov. 3</td>
<td>24 on Jan. 10</td>
<td>Predation and collecting</td>
</tr>
</tbody>
</table>

Eight birds were collected for examination from territory number 48 (table 52), and probably some others died from incidental shot wounds by Jan. 10. Fairly heavy pressure from enemies was noted during fall and winter, but it is very difficult to judge whether most of the loss from predation took place before or after the shooting. If most of the predation occurred before the population had been reduced by the shooting, then the carrying capacity of the territory would appear to be about 30 birds.

**TABLE 53. TERRITORY NO. 49 — BOONE, IOWA.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932·33</td>
<td>13 on Dec. 14</td>
<td>11 on Mar. 20</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1933·34</td>
<td>No data</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934·35</td>
<td>11 on Feb. 4</td>
<td>11 on Mar. 2</td>
<td>No loss</td>
</tr>
</tbody>
</table>

 Territory number 49 (table 53) is probably a distinct territory, though insufficient work was done on the surrounding lands to warrant placing it in Class One. Logan J. Bennett carried on the chief observational work on the Boone territories for the season of 1932-33.

**TABLE 54. TERRITORY NO. 50 — BOONE, IOWA.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932·33</td>
<td>9 on Dec. 14</td>
<td>8 on Mar. 20</td>
<td>Probably predation</td>
</tr>
<tr>
<td>1933·34</td>
<td>No data</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934·35</td>
<td>11 on Feb. 4</td>
<td>10 ? on Mar. 2</td>
<td>Predation</td>
</tr>
</tbody>
</table>
TABLE 55. TERRITORY NO. 51 — BOONE, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>30 on Dec. 14</td>
<td>25 on Mar. 20</td>
<td>Predation</td>
</tr>
<tr>
<td>1933-34</td>
<td>No data</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934-35</td>
<td>18 on Dec. 18</td>
<td>16 on Mar. 20</td>
<td>Predation; loss of 1</td>
</tr>
</tbody>
</table>

Territories number 50 and number 51 (tables 54 and 55) were situated in the bottom lands of the Des Moines River adjacent to other territories not kept under observation but unquestionably occupied. Hence, we have no way of determining the extent to which interchange between censused and uncensused coveys may have taken place, or what proportion of a common population range may have been represented by the observed territories.

TABLE 56. TERRITORY NO. 52 — VICINITY OF 37TH ST. AND UNIVERSITY AVENUE, DES MOINES, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1931-32</td>
<td>10 in Feb.</td>
<td>7 by April</td>
<td>Probably egress</td>
</tr>
<tr>
<td>1932-33</td>
<td>11 on Dec. 16</td>
<td>10 on Mar. 20</td>
<td>Probably egress</td>
</tr>
</tbody>
</table>

Certain of the residential sections of Des Moines furnish regular wintering territories for bob-white coveys. The birds have access to good cover in the wooded ravines of many backyards and they feed largely in gardens or at stations maintained for them. For the 1931-32 figures of territory number 52 (table 56) we are indebted to the notes of Mrs. John E. Stewart; these birds represented a covey which frequented her backyard and which were especially convenient for study [Errington (24)]. The apparent egress of 3 birds by April was attributed to restlessness attending the approach of the breeding season.

Dr. H. H. Knight, of Iowa State College, has since 1925 kept notes on the quail frequenting his backyard at 133 South Riverside, Ames, Iowa. His survival and wintering notes are here-with condensed for examination (table 57).

TABLE 57. TERRITORY NO. 53 — AMES, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1925-26</td>
<td>16 by Oct.</td>
<td>16 by Feb.</td>
<td></td>
</tr>
<tr>
<td>1926-27</td>
<td>16 by Oct.</td>
<td>16 by Feb.</td>
<td></td>
</tr>
<tr>
<td>1927-28</td>
<td>17 by Oct.</td>
<td>No apparent loss during winter</td>
<td></td>
</tr>
<tr>
<td>1928-29</td>
<td>13 on Sept. 15</td>
<td>11 by Feb.</td>
<td></td>
</tr>
<tr>
<td>1929-30</td>
<td>No fall count</td>
<td>11 by Jan. 11</td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>Exact territory not occupied; see text</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>15 on Jan. 20</td>
<td>15 on Mar. 6</td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>Territory occupied by 14 or 15 but notes not kept</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>14 by Dec.</td>
<td>No apparent loss during winter</td>
<td>Disappeared; possibly trapped</td>
</tr>
<tr>
<td>1934-35</td>
<td>13 on Dec. 15</td>
<td>0 by Jan. 7</td>
<td></td>
</tr>
</tbody>
</table>
Dr. Knight's notes (table 57) point to a gradual decline in carrying capacity or local environmental attractiveness beginning about 1928. The decline was probably not as abrupt as the impression from the 1928 to 1931 figures may at first indicate; in actuality, during these three seasons when there were fewer quail recorded in the immediate vicinity of the Knight home, there were more quail noted in the general neighborhood.

In 1928-29, a covey of 14 ranged not far distant in territory not known to have been occupied previously. In 1929-30, we suspect that there may have been a similar distribution, though it is not mentioned in the notes. The summer of 1930 was very dry, and in August fire swept the territory, ruining it for winter occupancy by quail; there were noted on Dec. 15, however, coveys of 11 and 16 in a cornfield to the south, which may correspond to those presumably evicted by the fire.

SURVIVAL DATA—EMERGENCY TERRITORIES

(Data from territories usually occupied but one season out of three to six and then only because of apparent necessity; the territories were usually deficient in cover although possessed of enough food to attract coveys evicted by agricultural practices, coveys crowded out of regular habitats by excessive densities of their own species or by other species such as pheasants, or coveys forced into precarious situations by hunger.)

TABLE 58. TERRITORY NO. 54—PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1931-32</td>
<td>26 on Dec. 17</td>
<td>19 on Mar. 5</td>
<td>Predation and poaching</td>
</tr>
<tr>
<td>1934-35</td>
<td>24 on Dec. 15</td>
<td>12 on Mar. 18</td>
<td>Predation</td>
</tr>
</tbody>
</table>

Territory number 54 (table 58), while occupied but two out of the six seasons it has been observed, nevertheless represents fairly habitable quail range. It may be recalled from the discussion under territory number 6, that territory number 54 may be looked upon as something of an offshoot, the occupancy of the latter being forced by overcrowding of the favored territory number 6. In 1934-35 the continued occupancy of number 15 at a point very close to number 6 probably lowered the carrying capacity of both number 6 and number 54.

TABLE 59. TERRITORY NO. 55—PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1933-34</td>
<td>17 on Nov. 21</td>
<td>12 on Feb. 10</td>
<td>Predation</td>
</tr>
</tbody>
</table>

Territory number 55 (table 59) was vacated by the surviving 12 after Feb. 10. It was occupied one season out of six.
TABLE 60. TERRITORY NO. 56 — PRAIRIE DU SAC, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1933-34</td>
<td>22 on Dec. 8</td>
<td>7 on Jan. 9</td>
<td>Predation and egress</td>
</tr>
</tbody>
</table>

The 7 birds surviving in territory number 56 (table 60) by Jan. 9 joined the population occupying the adjacent territory number 18, thereby bringing about an over-populated condition for that territory as well. Prior to the influx of the 7 from territory number 56, territory number 18 had had but 18 birds which it apparently was accommodating without difficulty; within approximately a month after the seven had joined, four birds were lost, and later one more, bringing the total surviving in territory number 18 down to 20 by March 19.

TABLE 61. TERRITORY NO. 57 — MCFARLAND, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>6 on Dec. 6</td>
<td>0 by Jan. 13</td>
<td>Starvation</td>
</tr>
</tbody>
</table>

The birds simplystarved out of territory number 57 (table 61) during the season of 1929-30, but quail made no known attempts to occupy it during the following season, despite a visibly better food supply.

TABLE 62. TERRITORY NO. 58 — PINE BLUFF, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1931-32</td>
<td>31 on Jan. 27</td>
<td>19 on Mar. 15</td>
<td>Largely predation</td>
</tr>
</tbody>
</table>

Territory number 58 (table 62) is comparable to territory number 54 in that it could be described as something of an offshoot of the more favored territory number 30. It, too, seemed to be fairly habitable—at least in the one out of three seasons it was known to be occupied—but the common range represented by number 58 and the adjacent number 30 was plainly over-populated. (For an account in more detail, see text for territory number 30.)

TABLE 63. TERRITORY NO. 59 — PINE BLUFF, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1931-32</td>
<td>17 on Jan. 5</td>
<td>12 on Mar. 15</td>
<td>Probably predation</td>
</tr>
</tbody>
</table>

Territory number 59 (table 63) was occupied one out of three seasons. It may be compared to a small island of passably habitable environment surrounded by extensive spaces uncongenial for wintering quail. The food and cover combinations were such that the covey frequenting the place in 1931-32 had few alternative courses of action in the event of attack by predators and hence was, to some extent, vulnerable.
TABLE 64. TERRITORY NO. 60—DESMOINES, IOWA, WATERWORKS SUPPLY GROUNDS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1933-34</td>
<td>7 on Jan. 12</td>
<td>0 by Feb. 27</td>
<td>Predation and egress</td>
</tr>
</tbody>
</table>

The small covey of 7 indicated for territory number 60, (table 64) seemed confined as long as it lasted to a narrow irregular strip of land bordering and penetrating territories number 10, number 23 and number 24. We are not at all sure that we have accurately pieced together the story of what happened here, but we think that this was a covey forced to wander from one unsatisfactory covert to another by reason of the better territories being already occupied to capacity. At any rate, the most evidence of predation found in the entire observational area (two kills) was found in territory number 60, and the covey finally disappeared completely.

SURVIVAL DATA—FORTUITOUS OR BUILT-UP TERRITORIES

(Data from territories occupied mainly by coveys establishing and maintaining themselves by chance or by adaptiveness in places usually not frequented; data also from usually uninhabitable territories made habitable through human activities, whether through accident or intent.)

TABLE 65. TERRITORY NO. 61—PINE BLUFF, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>18 on Jan. 25</td>
<td>0 by Mar. 22</td>
<td>Egress after Mar. 3</td>
</tr>
</tbody>
</table>

Territory number 61 (table 65) was made habitable for the one season of the three observed by grain-bearing manure spread near enough to a grapevine-grown fencerow to be accessible. The birds wintered from Jan. 25 to Mar. 3 without loss, but thereafter moved into territory number 30 which had been virtually depopulated by an earlier starvation crisis.

Territory number 62, at Prairie du Sac, Wis., was occupied for about the same reason as territory number 61 except that the quail subsisted on grain which they picked out of hog manure from a pasture. A covey of 12 was counted Dec. 24, 1929, and it seemed well situated for the winter, although no exact counts were obtained afterward.

Territory number 63, Pine Bluff, Wis., was made habitable during 1929-30, one winter out of three, by the clumping of a load of grain screenings beside a road at the edge of a woodlot. When first noticed, Feb. 3, 8 birds were taking advantage of this very welcome source of food in an area where there was much starvation. One month later, apparently the same number of birds were still scratching grain out of the pile.

Territory number 64, Denzer, Wis., was occupied one season out of three, and then, to appearances, only because a farmer had left a few corn-bearing shocks near a wooded bluff.
On Nov. 30, 1929, a count of about a half dozen was secured; 7 on Dec. 15; no actual counts thereafter, but the "sign" indicated that the covey wintered safely.

TABLE 66. TERRITORY NO. 65 — PINE BLUFF, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>13 on Jan. 25</td>
<td>18 on Mar. 27</td>
<td>Influx of 5; some loss</td>
</tr>
</tbody>
</table>

The birds occupying territory number 65 (table 66) showed exceptional adaptiveness for this locality. This is the only covey recorded in the Wisconsin notes as having survived in a corn field territory without brushy cover or without at least dense marshy growths or weed patches. The birds used partly open corn shocks—favoring two in particular of the dozen or more available—in lieu of the usual cover types. That this brushless environment had a certain temporary attractiveness is proved by the continued influx of birds during the late winter and the scant evidence of mortality suffered (the only bird found dead was a traffic victim on an adjacent highway).

It might be remarked parenthetically that the wintering of quail away from brushy cover is not of such infrequent occurrence in central Iowa as it appears to be in southern Wisconsin. Bob-whites on the more open central Iowa observational areas, at stable population levels corresponding to those of the semi-wooded southern Wisconsin areas, doubtless have adapted themselves to exist with less cover than birds not faced by as great necessity to do so. Comparatively few Iowa coveys, nevertheless, have demonstrated any decided ability to thrive in corn fields devoid of cover other than that furnished by cornstalks and weeds or by shocks.

TABLE 67. TERRITORY NO. 66 — ROXBURY, WIS.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>21 on Nov. 2</td>
<td>17 on Feb. 1</td>
<td>Probably predation before Dec. 24</td>
</tr>
</tbody>
</table>

Territory number 66 (table 67) was a farmyard and adjacent environment. The territory as a whole had been so closely grazed and so severely debrushed that it could hardly have been habitable for a covey of less adaptive living routine. As it was, the birds lived mainly about the farm buildings (their favored roost was in a cellar) and about the little brushy cover still remaining. They were protected and fed, and for a number of successive winters the territory had been occupied.

The covey was said to have been wiped out by pot-shooters late in the winter of 1929-30. At any rate, the birds disappeared and none were known to have reestablished themselves about the farmyard by the time that inspections were discontinued 3 years later. There were other occupied territories in the neigh-
borhood during the following winters, but no more birds developed quite the same habit of intimacy with man.

This instance is rather typical of the history of many barnyard territories. Commonly, birds are forced by hunger to enter farmyards presumably strange to them; if they are unmolested and find an accessible food supply, they doubtless come more readily the next time a starvation crisis presents itself; finally, they may simply accept the farmyard as a territory and may regularly establish themselves there at the time of the fall territorial adjustment. In a community where feeding of bob-whites in farmyards or about buildings is general, it is highly probable that most coveys are first led in by old birds which have had previous experience—mere boldness on the part of the leading birds does not alone explain the evident familiarity with the grounds often displayed.

TABLE 68. TERRITORY NO. 67 — OTTUMWA, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>22 on Dec. 7</td>
<td>17 on Mar. 22</td>
<td>Egress or mortality after Feb. 11</td>
</tr>
<tr>
<td>1933-34</td>
<td>15 on Nov. 19</td>
<td>22 on Feb. 19</td>
<td>Influx probably from No. 68</td>
</tr>
<tr>
<td>1934-35</td>
<td>28 on Nov. 17</td>
<td>17 on Jan. 27</td>
<td>Starvation and predation</td>
</tr>
</tbody>
</table>

Territory number 67 (table 68) was a barnyard territory near Ottumwa, Iowa. It was deliberately strengthened in 1932 by the planting of a cane food patch nearby. The 22 birds present in 1932-33, with no recorded change until mid-February or later, probably represents very nearly carrying capacity. In 1933-34, the territory seemed under-populated at first but was situated in an area generally over-populated; the subsequent influx, then, was not unexpected and by February had filled up the territory to about the same as the year before at this time. Chinch bugs and drouth ruined the food patch for the season of 1934-35.

Territories number 67 and 68 (table 69) were part of a game demonstration area established on private farmland by the Iowa Fish and Game Commission. Most of the quail counts for 1932-33 were made by deputy wardens and were taken from the office files of the Commission.

TABLE 69. TERRITORY NO. 68 — OTTUMWA, IOWA.

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>18 on Feb. 11</td>
<td>14 on Mar. 22</td>
<td>Unknown; data incomplete</td>
</tr>
<tr>
<td>1933-34</td>
<td>36 on Nov. 21</td>
<td>24 on Feb. 19</td>
<td>Egress and predation</td>
</tr>
<tr>
<td>1934-35</td>
<td>10 on Nov. 17</td>
<td>0 by Dec. 8</td>
<td>Starvation</td>
</tr>
</tbody>
</table>

It is very probable that much of the 1933-34 egress from territory number 68 (table 69) resulted from birds moving into the adjacent farmyard territory number 67.
The history of territory number 68 is extremely significant, as it furnishes a concrete example of how environmental carrying capacity for winter bob-whites may be raised—a very different thing from simply increasing the security of populations already within the carrying capacity of the land. By the planting of a patch of cane in an opening in a large woodlot, an entirely new habitable territory was created. This place formerly had not been regularly occupied, and it was at a sufficient distance from neighboring occupied territories as not to detract appreciably from their carrying capacities.

While inadequate records were kept for the first season (1932-33) of the food planting and while the drought ruined it for 1934-35, the data for 1933-34 indicate that more birds were thereby accommodated than had been possible before. Although the improvised territory was doubtless over-populated early in the season, the 24 birds wintering there were 24 that probably would not have survived otherwise. It is true that we cannot be too sure of what might have happened had there been no food patch in 1933-34, but we have contemporaneous data on surrounding populations which lost heavily because of overcrowding as matters were.

The birds filling up the new territory, number 68, in the fall of 1933 were very likely some that spent a great deal of their time ranging in the woods. We have found that the vast majority of so-called "wood coveys" on our Wisconsin and Iowa observational areas were only partially woods-dwelling, and were at least partially dependent upon cultivated grains or seeds of certain field weeds for food. Granted that the quail of territory number 68, deprived of the cane, might have picked up a comfortable living on squirrel-opened acorns for a substantial part of the season, it is not improbable that sooner or later they would have had to go elsewhere. The availability of the food patch could hardly have had any effect other than to relieve the congestion in neighboring territories, with a consequent lessening of wintering mortality.

SURVIVAL DATA FROM LARGE AREAS

It has been shown that a territory may exhibit a greater definiteness of winter carrying capacity when considered with adjacent territories collectively rather than when considered individually. This is especially true in areas where interchange of birds between coveys takes place more or less constantly throughout the winter. Carrying capacity under these conditions does not appear to be so much a property of a specific territory as it is a property of a collective land unit embracing a number of adjacent or neighboring territories.

For example, the collective unit composed of the adjacent
territories number 4, number 17, number 18 and number 19 (table 22) has shown a uniformity of carrying capacity not evident in any constituent territory by itself. Similarly, those of the Class Four territories upon which there have been varying survivals have been territories situated at the borders of observational areas, adjacent to territories not under observation and with which they may have formed territorial combinations of more definite carrying capacity. This is rendered more likely by the fact that practically all of the data which may be judged contradictory to the concept of year to year definiteness of winter carrying capacity are those that are under the greatest suspicion of being incomplete.

On the same basis may be explained the indefiniteness of carrying capacity shown by the problematical area "A" in the original presentation of data for consecutive seasons [Errington (26), table at the bottom of page 113 misplaced in printing from between fourth and fifth lines at the top of page 114]. Split up for more thorough analysis, the published data from area "A" are derived from territory number 2, which is a distinct aggregate of known covey ranges, and from territory number 45, which adjoined quail-occupied and uncensused agricultural land and hence had an indistinct identity as a territory. The reliable data from number 2 show uniformity of carrying capacity; the questionable data from number 45 do not.

Obviously, the larger the environmental unit under close observation, or the more isolated it is from neighboring units, the less will be the likelihood of error being introduced by unknown happenings in borderline territories. Obviously, also, the larger the unit the greater will be the likelihood of the unit containing complete rather than incomplete territories and incomplete combinations of territories.

The most significant data of this sort in existence come from Prairie du Sac, Wis., where an area of 5 square miles has been kept under observation for six consecutive winters. The data from this area have been published in some detail for the six seasons [Errington (20), (23), (32); Errington and Hamerstrom (35)].

Taken collectively, the Prairie du Sac survival data for the winters of 1929-30 and 1930-31 indicate that the wintering populations had not yet recovered sufficiently from the starvation losses of 1928-29 to exceed the carrying capacity of the land. The loss from predation of 5.8 percent per 90 days of the 1929-30 population of 121 birds and the 5.4 percent predation rate for the 257 birds of 1930-31 signify a substantial security under ordinary conditions for the populations wintering at these levels.

The first inkling of the precise carrying capacity of the 5
square miles at Prairie du Sac was gained at the conclusion of the 1931-32 season. A 400-bird population suffered a predation rate of 12.5 percent per 90 days, enough to reduce the wintering population to the vicinity of 329 birds by spring. Actually, a starvation loss of about 39 birds occurred, but the starvation represented an emergency so late in the winter that, for purposes of calculating survival levels for the best of conditions, it may be neglected. It is plain that, except for the emergency, practically all of the 39 starved birds would have survived—hence, carrying capacity for 1931-32 was virtually demonstrated at 329 birds.

For 1932-33, a season attended by no severe starvation or other emergencies, the survival was about 339 of an initial 406 birds, the predation rate of 12.7 percent per 90 days being similar to that of 12.5 percent for the similar population of 1931-32.

The winter carrying capacity for the area for the first 4 years of field study, then, apparently fluctuated slightly around 330 birds.

The carrying capacity of the area was doubtless lowered by the wholesale debrushing of roadsides carried on in December, 1933, by CWA relief labor. The habitability of a number of covey territories was not only impaired but in some cases virtually destroyed, and the coveys were evicted or rendered vulnerable to depredations of natural enemies.

By spring of the 1933-34 season, the surviving population was but 288 of an initial 433, the predation rate having been accelerated to 24.4 percent per 90 days. The 288 survival probably is not far from the carrying capacity of the area as it now exists, since the December roadside debrushing seemed to evict the equivalent of about two coveys.

The season of 1934-35 was attended by pronounced emergency conditions [Errington (32)], and the resulting data must be examined very critically if they are to be given any significance from the standpoint of carrying capacity. Prior to the beginning of the fall studies, the quail in this part of Wisconsin had been subjected to a short shooting season, but so few birds were known to have been bagged in the area that the net effect of the shooting was in all likelihood negligible. Food shortage and severe weather constituted the complicating factors.

Out of an initial late fall and early winter population established at 411 birds, only 196 were still on the area by spring. Of the 215-bird decrease, a total of 39 apparently moved out of the area; the balance of 176 were evidently lost, and, in addition, 8 birds that appeared to come into territory number 39 from the outside. Of the 176-bird decrease, representing mortality of the initial population, the loss of about 20 was attributed on fair evidence to starvation following an ice storm in January and 40 more to a blizzard which struck at the end of
February and left severe losses behind it, notably in territories number 5 and number 38.

The loss from predation on the Prairie du Sac area for 1934-35 was approximately 100 birds over an average observational period of 107 days, or at a rate of 20.5 percent per 90 days. The preponderance of the predation losses occurred in territories associated with number 6 (including number 12, number 15, number 16, number 54) and in territories number 4, number 13, number 14 and number 29, all of which were heavily overpopulated, either at the beginning of the season or by reason of the forced influx of birds driven from territories number 19, number 20 and number 39 by winter food crises.

Study of the data, from those territories or groups of territories mainly occupied during 1934-35, shows that, except for the starvation variable, the territories accommodated, with security from predators, just about the population levels one might have expected from their past history. The winter survivals for 1934-35 of the regularly occupied territory groups in Classes One to Three may be compared with their average demonstrated median\(^6\) survivals of the preceding years (table 70):

<table>
<thead>
<tr>
<th>Territory number</th>
<th>1st Count 1934-35</th>
<th>Final count 1934-35</th>
<th>Median car. cap. 1929-34</th>
<th>Chief cause of 1934-35 losses</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. 1</td>
<td>11</td>
<td>16</td>
<td>17</td>
<td>Interchange</td>
</tr>
<tr>
<td>No. 5 and No. 13</td>
<td>92</td>
<td>54</td>
<td>105*</td>
<td>Egress and starvation; predation in No. 13</td>
</tr>
<tr>
<td>Nos. 6, 12, 15, 16 and 54</td>
<td>72</td>
<td>50</td>
<td>53</td>
<td>Predation</td>
</tr>
<tr>
<td>No. 14</td>
<td>17</td>
<td>0</td>
<td>lethal</td>
<td>Egress and unknown</td>
</tr>
<tr>
<td>Nos. 4, 17, 18, and 19</td>
<td>91</td>
<td>59</td>
<td>59</td>
<td>Predation and egress</td>
</tr>
<tr>
<td>No. 20</td>
<td>18</td>
<td>0</td>
<td>21</td>
<td>Egress; food crisis</td>
</tr>
<tr>
<td>No. 29</td>
<td>27</td>
<td>16</td>
<td>17**</td>
<td>Probably predation</td>
</tr>
</tbody>
</table>

* For the three years during which the territories were most nearly filled.
** Estimated carrying capacity.

A comparison of columns three and four in table 70 proves that the 1934-35 survivals for territories in which predation was the principal cause of loss checked closely with the carrying capacities as previously determined. This is notably significant in view of the population shifting and massing precipitated by the emergency conditions.

Territory number 1 (see tabular data and pertinent discussions) suffered no detected loss from predation for the apparent reason that the dispersal of the drifting birds about as fast as they came in (from number 5 and number 39 in particular) rarely permitted top-heavy concentrations to endure for a dangerous length of time. The lethal record of number 12 for 1934-35 was probably due to the over-populated condi-

---

\(^6\) In cases where there was no true median the observed count closest to the median was used.
tion of the territories associated with number 6 to which it was adjacent and of which, in actuality, it comprised a part. Roadside debrushing during 1933-34 apparently wrecked what carrying capacity number 13 ever had in the first place. Territory number 14 was the well known lethal and was not expected to winter any birds. The drop of four birds for territory number 15 does not represent mortality or any lowering of carrying capacity; so far as we could see the birds simply made a late winter shift to a neighboring territory.

The larger territory groups such as number 6 and associated territories of number 13, number 15, number 16 and number 54 (table 7) and the number 4, number 17, number 18, number 19 group (table 22) revealed again an essential definiteness of carrying capacity corresponding to the median obtained from the annual survival figures.

**BANDING RESULTS COMPARED WITH OBSERVATIONAL CENSUS DATA**

It was made a general policy not to do much banding or collecting on the areas where populations were to be observed under conditions as natural as possible. Banding, itself, is not considered a very disturbing factor, but the necessary winter baiting of the traps plainly influences covey routine to some extent. For this reason, banding operations were largely restricted to an area near Madison, Wis., where the usual type of survival studies so far described were not carried on at the time.

We have for this area substantial data for three consecutive seasons: Observational data for the first, and banding data for the last two. The observational data were obtained by Errington during the winter of 1929-30. The banding data are on file in the office of Prof. George Wagner of the University of Wisconsin and represent the work of a number of cooperators, particularly H. G. Anderson, from 1930 to 1932 [Errington (18)].

Trapping and banding have the great advantage of proving beyond question what individual birds an investigator may be dealing with. Their chief drawback has to do with the virtual impossibility of catching all of the birds in an area at times when that is most desired. While most bob-whites may be easily trapped for the first time under favorable conditions, and while many individuals become habitual "repeaters," some birds become decidedly "trap-wise" after the fright of having been caught and handled once and only with difficulty are caught thereafter.

We feel, however, that the intensive winter banding records to which we have access give a nearly accurate total of the number of birds frequenting this one area for the seasons indicated
and that they demonstrate certain covey movements, but that, so far as survival data are concerned, they are inferior to our notes from field observations. It is plainly easier to locate and secure a count on an ordinary covey of birds than to get that covey into a trap, particularly if it is not pressed for food.

**TABLE 71. TERRITORY NO. 69 — UNIVERSITY MARSH FARM, MADISON, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>40 on Nov. 20</td>
<td>57 on Mar. 2</td>
<td>Influx</td>
</tr>
<tr>
<td>1930-31</td>
<td>57 banded birds recorded during winter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>47 banded birds recorded during winter</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Influx of a border covey of 19 about Jan. 15 was responsible for the 1929-30 population rise for territory number 69 (table 71).

**TABLE 72. TERRITORY NO. 70 — UNIVERSITY MARSH FARM, MADISON, WIS.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>43 on Nov. 20</td>
<td>38 on Mar. 2</td>
<td>Mainly predation</td>
</tr>
<tr>
<td>1930-31</td>
<td>37 banded birds recorded during winter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>54 banded birds recorded during winter</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

There was an apparent shifting of population from territory number 69 (table 71) to the adjacent number 70 (table 72) early in the season of 1931-32. This was presumably due to human activities in connection with extensive building operations in what had formerly been regularly occupied quail range. That the driving out of the birds in this case did not necessarily constitute lethal eviction is indicated by the data from the two adjacent territories combined (table 73):

**TABLE 73. TERRITORIES NO. 69 AND NO. 70 COMBINED.**

<table>
<thead>
<tr>
<th>Season</th>
<th>First count</th>
<th>Final count</th>
<th>Cause of difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>83 on Nov. 20</td>
<td>95 on Mar. 2</td>
<td>Influx and predation</td>
</tr>
<tr>
<td>1930-31</td>
<td>94 banded birds recorded during winter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>101 banded birds recorded during winter</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Some slight allowance should be made for the possibility of birds escaping the banding traps on territories number 69 and number 70, but the totals recorded for 1930-31 and 1931-82 are probably not far from the total numbers of resident birds. No wintering losses were noted during the season of 1930-31, but a loss of at least two was known to have occurred in 1931-32. All in all, it seems as if the survivals for the one observational and the two banding seasons on the adjacent territories match up in the vicinity of 95 birds (table 73). Ninety-five birds, then, we would say is very close to the winter carrying capacity of the combined territories or the carrying capacity of this area as a whole as it has existed for the period of our studies.
PART III. ANALYSIS OF CARRYING CAPACITY

UNIFORMITY OF WINTER CARRYING CAPACITY

Stoddard (70 p. 171) has already pointed out that a covey of quail may occupy a favored area of ground year after year with little or no increase in numbers. He goes on further to state:

"Evidence [from banding data] is at hand to show that every member of a covey in one of these favored ranges may wander away during the nesting season; that the covey occupying the range the following winter is made up of birds of neighboring coveys and their offspring; and that at best, a very few birds of any covey occupy the same range from year to year."

The more limited banding data from Wisconsin [Errington (18)] confirm those of Stoddard and support the conclusion that ".... the redistribution of the adult quail population after the breeding season, within limits of a half or three-quarters mile or even greater radius, may be to no small degree fortuitous; a bird spending the entire winter within a quarter-mile or less of the center of the covey territory may the next season winter in a territory possibly a couple of miles away. In other words an individual bob-white may continue to live in approximately the same place from year to year, or it may not."

It should then be plain that the occupancy of a given territory by the same apparent number of birds for a succession of seasons by no means proves that the territory is occupied by the same birds one season after another. Why a given territory should hold a maximum of only about so many birds is not so plain.

Stoddard (70 p. 170) says that by repeated combinations the coveys tend to keep their organization of normal size. We in our northern studies have found this to be one of the factors operative. But what determines this "normal size"? Why is 10 to 12 normal for the covey that occupies a given territory; why is some other number normal for still another territory?

We admit that we do not know the answer, nor can we advance what seems to us a reasonable hypothesis. We can, however, submit what data we have for critical examination, if only to permit clearer definition of the problems.

Winter carrying capacity roughly approximates the number of birds sufficiently well situated in their environment to be secure from enemies and to be adjusted with respect to intraspecific relations. If a population of sound individuals suffers severely from predation or if concentrations past a certain point are consistently reduced by the splitting off and departure of

7. We recommend the careful reading of Stoddard's excellent chapter on movements of bob-whites, pp. 167-182, for those who may be particularly interested in this phase of the subject.
birds, the evidence indicates a condition of overcrowding and insecurity, though the birds may be both strong and well-fed. Since reductions of over-populations to the comparatively secure winter equilibrium at the level of environmental carrying capacity are accomplished chiefly by predation and by egress, any sort of reliable determination of carrying capacity necessitates separate consideration of the losses due to predation and egress and the losses due to something else. This necessitates correcting the actual survival figures, to eliminate so far as possible the confusion caused by losses as from late winter starvation and other irregular or atypical emergencies. Allowances have to be made also for seasons during which wintering territories were under-populated and occasionally for seasons unproductive of scientifically acceptable data. The median survival figures for the individual territories or groups of territories probably give as close an approximation of the season to season carrying capacity as we are likely to obtain (table 74). Corrections in survival figures have been made, as indicated, on the basis of information previously given in the text in the discussions relating to the particular territories. All territories in the reliable Classes One to Three are eligible for consideration, in combination if not singly.

Table 74, presenting the survival figures for Classes One to Three in corrected form, provides what we consider an accurate picture of what would have been the full wintering survival on the various territories under non-emergency conditions. Under those conditions, the reduction of over-population is brought about simply by the failure of the environment to accommodate more than a certain number, season after season. The "median" of table 74 expresses approximately these accommodation limits. Populations in excess of this number seemingly are reduced through their vulnerability to predation or are forced by overcrowding into inferior environment elsewhere. In the latter event, excess populations are reduced anyway, usually through their vulnerability to predation in their new but inadequate range.

SEASONAL REDUCTION OF BOB-WHITE POPULATION SURPLUSES

If allowance is made for the variables introduced by starvation emergencies, atypical situations, territories under-populated or vacated voluntarily rather than through necessity, or any other cause except predation or egress forced by vulnerability to predation, it is to be seen that the preponderance of data

8. A state of under-population of a territory group is apparent when the population winters with security from predation but at a decidedly lower level than the level usually accommodated. Under-populations are, of course, most likely to occur in the wake of wholesale losses from starvation, over-shooting, drouth, etc.
from the superior Classes One to Three (territories number 1 to number 34) either support the concept of definiteness of carrying capacity or do not refute it. Neither may the concept be said to be refuted by the relatively inferior data of territories number 35 to number 70; indeed, from these it derives no small support, even from those data which superficially may appear contradictory.

All in all, what we are trying to get at in our attempts to analyze carrying capacity is: What is the population of adult bob-whites that a given habitat, as it usually exists from year
table 74. median survival or approximate season to season winter carrying capacity.

<table>
<thead>
<tr>
<th>Territory and median (on basis of corrected survival)</th>
<th>Season</th>
<th>Actual survival</th>
<th>Corrected survival</th>
<th>Reason for correction</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Territory No. 1 Median: 17</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1929-30</td>
<td>17</td>
<td>17</td>
<td>Late starvation of 12</td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>17</td>
<td>17</td>
<td>Late starvation of 12</td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>Territory under-populated</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>17</td>
<td>17</td>
<td>Late starvation of 12</td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>18</td>
<td>18</td>
<td>Late starvation of 12</td>
<td></td>
</tr>
<tr>
<td>1934-35</td>
<td>16</td>
<td>16</td>
<td>Late starvation of 12</td>
<td></td>
</tr>
<tr>
<td><strong>Territory No. 2 Median: 33</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1929-30</td>
<td>23</td>
<td>35</td>
<td>Late starvation of 12</td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>32</td>
<td>32</td>
<td>Late starvation of 12</td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>29</td>
<td>31</td>
<td>Loss from cold of 2</td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>33</td>
<td>33</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Territory No. 3 (In combination with No. 37) Median: 76</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>1929-30</td>
<td>Territory under-populated</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>about 77</td>
<td>about 77</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>about 76</td>
<td>about 76</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>Population evicted by man</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Territories No. 4, No. 17, No. 18, and No. 19 Combined Median: 59</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1929-30</td>
<td>Territory under-populated</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>60</td>
<td>60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
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<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>59</td>
<td>59</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>51</td>
<td>56</td>
<td>Loss of 5 probably due to eviction by man</td>
<td></td>
</tr>
<tr>
<td>1934-35</td>
<td>59</td>
<td>59</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Territories No. 5 and No. 13 Combined Median: 105</strong></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>1929-30</td>
<td>Territory under-populated</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>Territory under-populated</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>Territory under-populated</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>111</td>
<td>111</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>105</td>
<td>105</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934-35</td>
<td>54</td>
<td>96</td>
<td>Starvation and egress of about 42</td>
<td></td>
</tr>
<tr>
<td><strong>Territories No. 6, No. 12, No. 15, No. 16, and No. 54 Combined Median: 53</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1929-30</td>
<td>Territory under-populated</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1930-31</td>
<td>62</td>
<td>58</td>
<td>Later loss of 4</td>
<td></td>
</tr>
<tr>
<td>1931-32</td>
<td>46</td>
<td>52</td>
<td>Loss of 6 from shooting, etc.</td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>53</td>
<td>53</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>66</td>
<td>66</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934-35</td>
<td>50</td>
<td>50</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Territory No. 7 Median: 48 (?)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>51</td>
<td>51</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>38</td>
<td>38</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934-35</td>
<td>0</td>
<td>48</td>
<td>Eviction</td>
<td></td>
</tr>
<tr>
<td><strong>Territory No. 8 Median: 20 (?)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>20</td>
<td>20</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>21 (?)</td>
<td>21 (?)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934-35</td>
<td>7</td>
<td>20 (?)</td>
<td>Atypical</td>
<td></td>
</tr>
<tr>
<td>Territory No. 9</td>
<td>Median: 20</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-----------------</td>
<td>------------</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1932-33</td>
<td>20</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1933-34</td>
<td>20</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1934-35</td>
<td>24</td>
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<table>
<thead>
<tr>
<th>Territory No. 10</th>
<th>Median: 54</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>55</td>
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<tr>
<td>1933-34</td>
<td>54</td>
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<tr>
<td>1934-35</td>
<td>54</td>
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</tbody>
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<table>
<thead>
<tr>
<th>Territory No. 11</th>
<th>Median: 30</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>30</td>
</tr>
<tr>
<td>1933-34</td>
<td>30</td>
</tr>
<tr>
<td>1934-35</td>
<td>30</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Territory No. 12</th>
<th>Median: 55</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>55</td>
</tr>
<tr>
<td>1933-34</td>
<td>55</td>
</tr>
<tr>
<td>1934-35</td>
<td>55</td>
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</table>

<table>
<thead>
<tr>
<th>Territory No. 13</th>
<th>Median: 30</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>30</td>
</tr>
<tr>
<td>1930-31</td>
<td>30</td>
</tr>
<tr>
<td>1931-32</td>
<td>30</td>
</tr>
<tr>
<td>1932-33</td>
<td>30</td>
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<tr>
<td>1933-34</td>
<td>30</td>
</tr>
<tr>
<td>1934-35</td>
<td>30</td>
</tr>
</tbody>
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<table>
<thead>
<tr>
<th>Territory No. 14</th>
<th>Median: 30</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
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<td>1930-31</td>
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<td>1931-32</td>
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<tr>
<td>1933-34</td>
<td>30</td>
</tr>
<tr>
<td>1934-35</td>
<td>30</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Territories No. 15 and No. 16</th>
<th>Median: 30</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>30</td>
</tr>
<tr>
<td>1930-31</td>
<td>30</td>
</tr>
<tr>
<td>1931-32</td>
<td>30</td>
</tr>
<tr>
<td>1932-33</td>
<td>30</td>
</tr>
<tr>
<td>1933-34</td>
<td>30</td>
</tr>
<tr>
<td>1934-35</td>
<td>30</td>
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</tbody>
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<table>
<thead>
<tr>
<th>Territories No. 17 to No. 19</th>
<th>Median: 30</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929-30</td>
<td>30</td>
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<tr>
<td>1930-31</td>
<td>30</td>
</tr>
<tr>
<td>1931-32</td>
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<td>1932-33</td>
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<tr>
<td>1933-34</td>
<td>30</td>
</tr>
<tr>
<td>1934-35</td>
<td>30</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Territory No. 20</th>
<th>Median: 21</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>5</td>
</tr>
<tr>
<td>1933-34</td>
<td>5</td>
</tr>
<tr>
<td>1934-35</td>
<td>5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Territory No. 21</th>
<th>Median: 5</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>5</td>
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<tr>
<td>1933-34</td>
<td>5</td>
</tr>
<tr>
<td>1934-35</td>
<td>5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Territory No. 22</th>
<th>Median: 15</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
<td>15</td>
</tr>
<tr>
<td>1933-34</td>
<td>15</td>
</tr>
<tr>
<td>1934-35</td>
<td>15</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Territory No. 23</th>
<th>Median: 15</th>
</tr>
</thead>
<tbody>
<tr>
<td>1932-33</td>
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* Mixed bob-whites and ring-necked pheasants [Errington (26)].
** Carrying capacity probably lowered for 1934-35 by the debrushing of a part of territory No. 13 the season before.
*** This figure may not have too much significance because of the late winter starvation mortality recorded in this territory for the 1929-30 season.
to year, can winter under optimum climatic conditions and what are the basic factors limiting the number that may be accommodated? The number that may be accommodated, as we have indicated, appears to be remarkably definite and represents the density which natural enemies are not able to reduce materially in the course of the winter. In other words, whatever else it may be, it represents the population which is intrinsically secure in its winter environment, both from simple predation and from eviction by predators.

A review of the survival data shows that the population densities surviving winter predation are far more uniform for specific territories or territory groups than are the densities which may be present at the beginning of the winter. The beginning densities are likely to be highly variable, though usually above rather than below the carrying capacity of the environment. In the vast majority of the many instances in which the initial recorded populations were below or up to (but not above) carrying capacity, slight further losses from predation alone were suffered. In most of these instances, the occurrence of densities at the level of carrying capacity as early as December or even November meant that the resident birds had already suffered about as much predation mortality as they were going to for the season.

We have listed 119 specific instances in which it was clear that territories had or should have (barring late starvation emergencies, etc.) wintered populations up to their carrying capacity. In 69 instances the territories had been almost exactly filled at the start of the season’s observations; in 43, the territories had been distinctly over-populated at the beginning; in 7, distinctly under-populated, to be filled during the winter.

The instances relating to initial over-populations are, to our way of thinking, the most significant. They demonstrate with inexorable clarity the instability of populations that exceed the capacity of the land to accommodate. Again and again, excess populations have been reduced by spring to the level of carrying capacity—whatever that may be for the specific territory or the aggregate of territories under observation.

Aside from losses of immature birds during the growing season, the strongest annual acceleration of predation upon bob-white seems to come in late autumn, when the habitability of large tracts of land is lowered by the falling of leaves from deciduous brush and by the drying up of much herbaceous plant growth. The reduction of cover is accentuated by the early snows, and evidences of predation may for a time be very conspicuous. Then, sooner or later, the surplus birds from the season’s breeding are killed or leave; and the remaining population enjoys a comparative security from ordinary simple predation until spring and presumably until there is again a surplus.
That the severity of fall and winter predation upon healthy adult birds is largely dependent upon the degree to which the environment is over-populated is indicated by experimental as well as by observational evidence. The artificial removal by shooting of surplus birds on Iowa game management areas in November, 1933, resulted in an apparent increase in security for the wintering populations. The populations on 10 shot areas collectively lost during the winter at the rate of 10.8 percent and those on the 4 unshot areas studied as checks lost at the rate of 28.3 percent [Errington and Hamerstrom (35)].

Our censuses of the shot populations in particular were beset by imperfections, yet the difference in winter loss rates on the shot and unshot areas surely points to some relief of the normally over-populated fall condition as a result of the shooting. This is precisely what one might expect theoretically, although the effects of shooting and of natural predation upon an over-population differ in significant respects.

Predation is infinitely more selective of vulnerably situated birds than shooting, for the obvious reason that man, by means of trained dogs and modern firearms alone, is capable of taking toll from bob-white populations that may be virtually secure from natural enemies. Moreover, natural enemies prey largely according to the comparative ease with which a prey species may be caught, and they tend to neglect species that no longer provide them profitable hunting; whereas man may prize a hunted species more because of its rarity and pursue it the more eagerly.

In nature the evidently increased security of normal winter bob-white populations, after they have been trimmed down by predation to fit the carrying capacities of the areas studied, indicates that the actual vulnerable surplus has been removed. In shooting for sport it is highly probable, even if the exact number corresponding to the seasonal surplus were taken, that pressure would be applied unevenly upon coveys both over-populating and under-populating their coverts. The shooting of an insufficient number of birds from an over-populated territory would still leave an over-population vulnerable to predation. The shooting of birds from territories capable of wintering the populations they have might leave some environment under-populated for the season, especially if the population as a whole has settled down to a rather circumscribed winter routine. This is probably as reasonable an explanation as any for the relatively high winter loss of 10.8 percent suffered by the populations on the experimentally shot areas, compared with the losses of secure unshot populations, which losses, as measured, commonly have not exceeded 6 percent.

Midwinter adjustments of bob-white populations between territories also reveal a close relationship between over-popula-
tion and vulnerability to predation. The splitting and recom-bining of coveys in a densely populated group of territories may be looked upon, at least in part, as a manifestation of uneasiness resulting from the possibility of too many birds occupying the same environment at the same time.

If more birds join a wintering covey, which had approximately filled the occupied territory to carrying capacity before the union, the covey (resident birds plus newcomers) may with comparative promptness suffer losses tending to trim down the over-population, that is, unless the over-population is relieved by the departure of the joining birds or by an equivalent number. The loss of the top-heavy surplus in most of the known instances has occurred within the few weeks following the influx. Sometimes tragedies of this sort have been repeated two or three or even more times in a given territory during the season and are particularly to be noted when remnants of coveys depleted by starvation or evicted from territories elsewhere attempt to find safer quarters.

If the territory entered happens to be strong and under-populated (as is infrequently the case by mid-winter), the newcomers may station themselves there with security. But if their influx means anything more than a temporary over-population for the territory and a compensatory egress is not made, some birds are practically sure to suffer from it.

PREDATION AND CARRYING CAPACITY

Publication of the mere fact that predation has proved to be a major medium in the reduction of bob-white over-populations almost inevitably serves to focus public attention upon predators rather than upon what predation signifies. It is difficult in the extreme for the public to recognize that, in this instance at least, predation is but a symptom and not a cause of biological unbalance.

The data which we have on bob-white losses and predator populations [see especially Errington (26)] indicate that within ordinary limits there is no evident relation between kinds and numbers of predators and the severity of predation upon bob-whites under natural winter conditions.

We do not say that exceptions to this generalization are not possible, actually as well as theoretically. It is, of course, easy to postulate that if there were no predators there could be no predation, but such speculation is idle. It may be counter-postulated with a great deal more biological basis that as long as there is abundant edible life some life will exist to eat it, though not necessarily the same species which we are in the habit of referring to as predators. Familiarity with the predaceous tendencies frequently displayed by large numbers of birds and mammals which are not commonly thought of as
predators leads one to suspect that practically any form of life may become predatory to some degree when the opportunity or the necessity presents itself. Predation, then, depends more upon the presence of something vulnerable as prey than upon the systematic position or the predilections of the animals which may do the preying.

It seems entirely reasonable to suppose that predation is a normal phenomenon associated with life, reflecting the reaction of hungry creatures to the food which happens to be most available. If we consider parasitism and predation together we may perhaps reasonably suppose also that the net pressure of these combined may not change vastly except as the vulnerability or the susceptibility of organisms to them changes.

Over-populations generally are conspicuous targets for attacks by predators or parasites. Nature may abhor a vacuum, but she abhors over-population not a great deal less. Someone has said that Nature has more than one arrow for her bow. Over-populations are insecure because they are over-populations. If they are not reduced by one thing they are by another.

In the case of the bob-white, the winter over-populations which we have studied have been reduced mainly by predation, but it by no means follows that they would not have been reduced had it not been for predators, or that reduction in numbers of the predators would have made the over-populations any more secure. The evidence is all to the contrary.

Territory number 14 furnishes one of the best cases in point. The predator population of this territory, in the course of the six winters during which it has been under observation, changed greatly in composition, both with respect to numbers and to species of predators present; yet the patently lethal character of the environment for wintering quail has not changed perceptibly. Fluctuations in numbers and species of predators have been apparent from one winter to another on practically all of the areas under regular observation [for examples, see Errington (26)], but the bob-white survival data have not shown any connection with these fluctuations.

Most of the season to season differences in predator populations on the observational areas have been due to natural causes, such as inter- and intra-specific relationships of the predators, losses among resident predators as from disease [Errington (16) and unpublished; Green and Shillinger (39)] and accident, irregularities of residence of migratory forms, etc., plus the usual sporadic shooting and trapping by the public. On a few of the areas, predators were deliberately encouraged; and on a few others, they were drastically campaigned against

9. Examples of primarily vegetarian groups which upon occasion may be conspicuously predaceous include gallinaceous birds (notably turkeys, pheasants, domestic chickens) and nearly all rodents.
Errington and Hamerstrom (35)]. But whether the winter predators were encouraged, left comparatively un molested, or actively persecuted, whether the predators were few or many, any effects that the resulting differences in predator populations may have had on winter survival data have been so slight as to be unmeasurable. This is well brought out by table 74 and by practically all of our survival figures for specific areas over considerable periods of time.

COMPENSATORY PRESSURE OF PREDATION ON BOB-WHITE POPULATION SURPLUS

Great horned owls (Bubo virginianus) and Cooper’s hawks (Accipiter cooperi) are two of the most formidable of quail enemies and the ones to which most of the known winter predation has been traced. On our observational areas, horned owls have probably killed more winter bob-whites than all of the other predators combined; Cooper’s hawks and marsh hawks (Circus budsonius) ranked a weak second and third and red and grey foxes (Vulpes fulva and Urocyon cinereoargenteus) a still weaker fourth, at least so far as concerns detected mortality. All of the many other species of predators studied, including the house cat (Felis domestica, of alien origin and bird-killing repute) have trailed far behind as known predators upon winter bob-whites.

Contrary to what would seem most reasonable at first glance, lower populations of the most formidable predatory types, down to scarcity or actual absence on the observational areas, has not resulted in any appreciable lessening of the net pressure of predation upon bob-white winter populations. The 1931-32 season showed terrific horned owl predation upon the occupants of the lethal territory number 14; in 1932-33, the horned owls were gone but the losses continued, this time through the medium of grey foxes; in 1933-34, the foxes were greatly reduced in numbers, but still the bob-white losses were annihilatory because of foxes and general predation. In other instances, predator populations have noticeably increased, sometimes to top-heavy peaks, without any apparent effect on bob-white survival as compared with other winters. Not once have we been able to establish a clear-cut case of differences in predator kinds and numbers having any net influence upon the losses from predation suffered by wintering bob-whites.

The one thing that seems really to count in determining the severity of the predation is the position of the quail population with respect to the carrying capacity of the land. This severity we have found to be quite predictable on areas having carrying

10. Stoddard, however, has found the Cooper’s hawk to be the supreme predatory quail enemy in the South, and the marsh hawk to be of negligible consequence. Both hawk species were abundant on his observational areas, though horned owls were fairly common and foxes uncommon.
capacities demonstrated by recorded survivals over a period of years, apart from complications brought on by starvation emergencies, destruction of habitats by wholesale debrushing, burning, fall plowing, heavy pasturing and the like.

Seemingly irrespective of the kinds and numbers of predators present, the severity of simple winter predation will depend upon how many quail there are beyond the carrying capacity of the land. For example, in table 74 the median of 17 may be taken as the carrying capacity for territory number 1; birds in excess of this approximate number will either have to leave or be killed. Even for the grouped territories number 6, number 12, number 15, number 16 and number 54, which show collective full survivals of such widely separated extremes as 50 and 66, the median of 53 is not far from the number of birds of a fall population which can be expected to survive any non-emergency winter.

If the wintering population is below the carrying capacity of the land, or just within it, light losses from simple predation may be predicted, in most cases not to exceed the rate of 6 percent per 90 days. Populations up to carrying capacity do not seem to suffer at proportionately higher loss rates than populations only partially filling the suitable winter environment available; at least, this appears true for well accommodated populations as high as a bird per four acres, which is the highest level that we have been able to census with required accuracy.

We have been gaining a general impression, as yet unsubstantiated by adequate data, that securely situated Iowa bobwhite populations suffer from predation at a slightly higher rate than corresponding Wisconsin densities in environments of corresponding carrying capacities. It may be that predation losses between 10 and 15 percent per 90 days for substantial populations within the median carrying capacity of the land may not be so exceptional. Our Iowa data are as a whole far less trustworthy than the data from Wisconsin, if only for the reason that at their best they cover but a 3-year period. Then, too, we cannot be too sure that the annual environmental changes due to central Iowa agricultural practices on larger land units may not bring about decided changes in carrying capacity from year to year. If central Iowa carrying capacity for quail does change decidedly from year to year, at best, survival for a given winter might fluctuate considerably from the median derived from data from consecutive seasons, in contrast with the greater uniformity of survival shown by populations on the more stable Wisconsin ranges.

For the present, however, we may feel fairly safe in predicting predation losses usually below 6 percent per 90 days for secure winter populations. A hypothetical area of 4,000 acres having a carrying capacity of a bird per four acres or 1,000
birds, would then lose from winter predation in the vicinity of 6 birds or less per 90 days of every 100 birds below 1,000. If the population on the given area exceeded carrying capacity, the loss would amount to the excess, or approximately 200 of a population of 1200; 500 of a population of 1500; 1000 of a population of 2000, etc.

Roughly, the birds over the thousand level in the above hypothetical area represent the surplus population for the area, and as a surplus they either have to move out or are doomed to be killed during the winter. A bob-white population does not have to be of high density to have a surplus; it only has to exceed the accommodating capacity of the environment, be that high or low. A population of no more than a bird per square mile may have a surplus, if the carrying capacity of the land is less.

Under ordinary conditions in Wisconsin and Iowa, the vulnerably situated surplus has been found to be reduced largely through the medium of the more efficient types of quail enemies, i.e., horned owls and the Cooper's hawks. When these forms are absent or present only in low densities, the reduction is apparently accomplished by enemies less adapted to prey upon quail, such as marsh hawks and foxes. In the absence of these, still less efficient quail enemies seem to exert a compensatory pressure.

Red-tail hawks (*Buteo borealis*) and barred owls (*Strix varia*) are species which, when competing with truly formidable predator types for a vulnerable bob-white surplus, are hardly to be classed as quail enemies. Nevertheless, these may on occasion prey rather conspicuously on bob-whites, presumably with enough force to reduce over-populations down to the usual level of secure accommodation. Clumsy dogs, weak owls, typically non-predaceous forms such as the ring-necked pheasant [*Leopold (46) p. 56*] and rat to squirrel-sized rodents, have all been known to kill adult quail; and in the aggregate these may conceivably be capable of considerable pressure on a bob-white surplus long enough exposed.

For that matter, the bob-white itself is not entirely beyond suspicion as a killer of, if not a predator upon, its own species [*Stoddard (70) p. 222*], to say nothing of the biological complications attendant upon over-crowding in restricted habitats. More than one species, upon analysis, proves to be the final check upon itself, in one way or another.

"BUFFER" POPULATIONS AND BOB-WHITE LOSSES FROM WINTER PREDATION

It has long been accepted practically without question that population densities of rodents and other "buffer" species have a profound influence upon the predation rate suffered by bob-
white. The predation rate upon bob-white has been thought to decline with rising buffer populations, and to rise with declining buffer populations.

Higher buffer populations have also been thought to have an indirect effect in increasing bob-white predation losses through the attracting of more predators into a given area, a logical corollary to the popularly held assumption that bob-white predation losses vary with the number of predators. It has further been thought that the subsequent decline of a buffer population which has built up a heavy density of predators is followed by increased pressure of the predators upon the resident bob-white population.

We do not say that there is no truth in the commonly accepted ideas expressed above. We do not say that they may not be entirely correct as to the relationship of buffer and predator populations to bob-white predation losses under some circumstances. Stoddard (letter, Aug. 27, 1935) ably defends the management practice of keeping down populations of cotton rats (Sigmodon spp.) on south-eastern quail lands as a means of discouraging predators which are incidentally egg eaters. He has uniform data on over 2,000 quail nests, compared with which our own data are altogether too limited and obscure to justify making many positive statements on this phase of the subject.

But the data from our Iowa and Wisconsin observational areas indicate that if there is any real balance between buffer and predator populations and winter predation upon bob-white, it is at least not a conspicuously delicate balance [Errington (26)]. We have no evidence which would lead us to suspect that fluctuations in buffer populations have played any part in either mitigating or increasing predator pressure on the particular bob-white populations with which we have been working.

Errington (15) published what he considered at the time to be an example of a quail population rendered vulnerable to horned owl pressure by reason of scarcity of rabbits and other usual horned owl prey, but a more critical analysis of the data suggests an over-population of quail for the territory (number 48 in this bulletin) instead of a significant under-population of buffers. In the same paper, the Wingra Wild Life Refuge was given as an example of an area having a quail population relatively secure from horned owl pressure because of a teeming rabbit population; whereas, in the light of present interpretation of the evidence, the security of the quail was due simply to the fact that they had not over-populated their environment (territory number 2, 1930-31).

While our methods of estimating buffer populations were admittedly crude [Errington (26)] and not at all to be compared in precision with our quail winter census technique, it
was nevertheless possible to get some idea of major fluctuations in rodent and rabbit numbers. We knew beyond question that there was in south-central Wisconsin a top-heavy abundance of meadow mice (*Microtus spp.*) in the summer of 1929 and the winter of 1929-30. We knew beyond question that this peak collapsed and that for the next 2 years very few meadow mice could be found in the observational areas. Conspicuous changes in the usual buffer fauna were to be noted in a number of localities during the course of the studies, whatever may have been our inability to record these changes with desired exactness.

But aside from any lack of relation between bob-white losses from predation and fluctuations of buffer and predator population densities as recognized or recorded, the apparent year to year definiteness of environmental carrying capacity for wintering bob-whites is in itself the strongest evidence against any close relation actually existing under ordinary conditions. Even if we did not know that buffer and predator populations had varied greatly in composition on the observational areas over a period of years, it would be asking a great deal of coincidence to postulate, on the grounds of uniformity of quail survival alone, that the population ratios of buffer and predator species had themselves remained uniform for area after area, year after year.

In connection with public or conversational discussions of bob-white population vulnerability, we have frequently been asked the question: "What do the predators eat when they can't catch the quail?"

When quail populations are too securely situated to be preyed upon, the predators eat the rodents, rabbits and other buffers or other over-populations which constitute the bulk of their diet anyway. Quail should be regarded as an incidental rather than as a staple food for predator populations under normal north-central states winter conditions. If there are surplus quail to be eaten, they seemingly will be eaten by something. If the wintering quail are securely situated, there is no surplus, and, granted that the birds are in good condition and ordinarily adaptive, they will suffer little loss. Whether there is no quail surplus available to predators, or whether the birds aren't there is of slight apparent consequence to the predators.

In short, it is more than probable that predators could get along very nicely if there were no bob-whites in existence, as there virtually are not in many localities within the geographic range of the bob-white as well as the range of the various predatory species. Bob-white populations at the maximum adult level of a bird per acre [Stoddard (70), Leopold (46)] still would not represent a chief source of food for predators generally, even if the entire quail populations were available. Actually, early winter populations in much of the best of southern
Iowa quail country run between a bird per 2 and a bird per 6 acres, of which populations the vulnerable surplus rarely exceeds 50 percent and seems more likely to average in the vicinity of 30 percent [Errington and Hamerstrom (35)]. Commonly, the wintering densities are more nearly a bird per 12 or 15 or 20 acres, with a still lower vulnerable surplus, which would mean rather slim picking for any considerable population of predators at all dependent upon bob-whites for food.

Some of our analyses of horned owl pellets have shown quail remains in as high a proportion as 15 percent of the pellets examined (unpublished). This represents terrific pressure, of an intensity sufficient to annihilate, in the course of a winter, coveys occupying such lethal territories as number 14 in 1931-32. It also represents the horned owl pressure applied to populations which for some reason have far exceeded the carrying capacities of their territories, as those of the number 6, number 12, number 15, number 16 and number 54 combination for 1934-35.

This incidence of quail remains in 15 percent of the owl pellets of given collections should not be misinterpreted as meaning that quail made up 15 percent of the diet of these owls for the period indicated by their pellets. Seldom would a pellet be composed entirely of quail remains, and in most cases remains of other prey would predominate. Hence, it would be more in keeping with accuracy to state that we have never known the diet of even a quail enemy as singularly efficient and as automatic in reaction as the great horned owl [Errington (21)] to be made up of more than about 5 percent of quail by bulk.

In our opinion, no other native predator can apply as much pressure upon a winter bob-white over-population as the horned owl. With bob-white constituting an observed maximum of not far from 5 percent by bulk of the horned owl's diet under the most favorable conditions for predation which we have been able to record, one may logically deduce that bob-white populations as they ordinarily occur do not go far in providing a source of food for hungry flesh-eaters. Whether the bob-whites may be plentiful, scarce, or absent, whether they may be secure or insecure, predator populations usually are able to subsist chiefly upon the rodents or rabbits or other so-called buffers which rarely fail to exceed by far the bob-whites in numbers and surpass them by far in availability.

The evidence which we have does not lead us to believe that predator populations, under the north-central states conditions which we have studied for the past 6 years, are likely to utilize anywhere near the food supply available to them. We have studied food habits of predatory species on a substantial scale in connection with our regular researches as times when staple prey species have been at high and at low levels.
It is quite apparent that the "Malthusian Principle" is not the principal factor in determining animal populations in nature [McAtee (60)], although it unquestionably is not without application. Animals certainly have been known to starve, especially under emergency conditions. There are clear instances of top-heavy populations having been reduced by starvation, but starvation does not appear to be the usual agency which holds most animal populations in check. So far as the predator populations which we have studied are concerned, the predators, with a few exceptions [see for example, Errington (11)], had enough to eat at all times, whether prey populations were comparatively low or comparatively high.

When the meadow mouse population of south-central Wisconsin was at its peak in 1929, meadow mice were killed and eaten in great quantities by a wide variety of animals, including crows, bitterns and domestic chickens; yet all of this predation made no perceptible impression upon the numbers of mice. After the meadow mouse population had obviously fallen to a level insignificant compared with what it had been, predators were still eating and were apparently getting along perfectly well on rabbits and deer mice (*Peromyscus spp.*) instead. Some species, notably long-eared owls (*Asio wilsonianus*), even continued to feed upon meadow mice in just about the same proportion as before [Errington (15)].

It seems, then, that a broad generalization may be made to the effect that the usually staple prey populations are usually much more than adequate to support predator populations of the kinds and densities that usually occur in the north-central states. Bob-whites, being rarely if ever staple prey for anything, may perhaps be regarded as but a side dish for hungry flesh-eaters, entirely acceptable if conveniently available, easily to be dispensed with if not.

**FOOD AND CARRYING CAPACITY**

Food is obviously one of the essential constituents of a habitable winter quail territory. Its role in determining the carrying capacity of quail environment should be carefully discussed, as this subject lends itself especially to popular misunderstanding.

It is true that the habitability of a wintering territory is closely correlated with the food supply, in the sense that there must be enough high quality food available to hold and feed the birds there. The amount necessary to sustain a wintering covey is comparatively small, however, in terms of bulk; and carrying capacity of bob-white environment does not vary directly with the amount of food, save exceptionally. Only under some emergency conditions or under those approximating the primitive, have we found survival delimited by the amount of food to be had during open winters.
The food situation for Iowa and Wisconsin quail seems typically characterized by two extremes. Either there is not enough food for any wintering population or there is a vast abundance of food far surpassing the needs of any quail population that could conceivably station itself in a circumscribed area. In Michigan, Dalke (6) gathered grains and weed seeds from 1,377 random samples (each of 4 square feet) on three sections of farm land on which he had been studying pheasants. He computed from these samples that an average of 6,303 pounds of edible material was available per square mile for fall and winter consumption by seed-eating animal life. That a supply such as this would not be left unmolested for a single species—quail or any other—stands to reason, but it would take a great many quail eating between two and four ounces a week to make much impression upon it.

Where there isn’t enough winter food for any population, it does not make a great deal of difference if a dozen birds or twice as many try to exist there. If the food supply is ample and regularly available to a quail population up to the demonstrated carrying capacity of the land, increasing the supply still more will not bring about a corresponding increase of carrying capacity. If the ecological scales are set so fine that there is no more than exactly enough for the wintering bob-white population, they may be thrown out of balance at almost anytime, anyway, as by the chance visitation of a numerous flock of sparrows or other small birds.

Territories or potential territories usually critically deficient in food are those on which, or near which, there is no cultivated land, or on which the foods resulting from cultivation have been removed by clean cropping, burning, or pasturing, or have been turned into the soil by fall plowing. Wild lands are particularly likely to be short of food, as well as lands reverted from cultivation. Native food of high winter sustenance value for bob-white may occasionally be very abundant according to the season, but they may also be very scarce. These include squirrel-opened acorns (Quercus spp.) certain of the Leguminosae, as tick trefoil (Desmodium grandiflorum) and hog peanut (Amphicarpa monoica), and jewel weed (Impatiens spp.). An exotic of similar irregular significance as quail food is the now naturalized black locust (Robinia pseudoacacia).

A distinction should be made between the substantial types of food which are essential to the quail as winter staples and the succulent or fruit-like types which are valuable more for their minerals, fruit acids, vitamins, etc., than for any energy-supplying qualities [Errington (12); Leopold (48)]. Unless a food is high in available protein, carbohydrate, or fat, it cannot be expected to provide the nourishment required by quail in cold weather. Quail starve in but a few days’ time when compelled, in confinement or in the wild, to rely too much for food
upon such common and readily eaten winter fruits as those of sumac (*Rhus* spp.), wild grape (*Vitis* spp.), bittersweet (*Celastrus scandens*) and Rose (*Rosa* spp.).

Man, through his settlement of the land has tremendously increased the supply of available quail food over that to be found under pre-settlement conditions, whatever may be the other effects of his use of the land. As a by-product of settlement, pigeon grass (*Setaria* spp.) and lesser ragweed (*Ambrosia artemesiifolia*) are two weeds which contribute materially to making present bob-white populations possible. Man’s cultivated corn (*Zea mays*) we find to be the supremely important winter quail food for our Wisconsin and Iowa areas, and soybeans and most small grains are important also.

Optimum conditions for Iowa quail seemed to exist about 1880. Since then, gradual intensification of farming practices has adversely affected quail environment from the standpoint of food. Unwise land use has even impoverished and wasted much of the food-productive top-soil itself. This granted, the food situation for bob-whites on cultivated land is still uniformly superior to that for the birds on uncultivated lands. Exceptions occur, of course, on wildlife refuges, etc., where adequate artificial feeding compensates for the deterioration of the food supply through plant succession and withdrawal from cultivation.

Let it be granted also that a drouth such as the one of 1934 [see Errington (29)] may drastically cut down if not wipe out the supply of quail food over wide areas, and that heavy snows or ice storms may cover up what little is left. The generalization can still be made with comparative accuracy that the year to year winter carrying capacity of environments for bob-white in Iowa and Wisconsin is not proportional to the amount of food. On most farms we have observed, there was usually, during open winter weather, food enough to feed many times the peak number of quail that we have found, and enough more to feed the variable numbers of small birds and small mammals which occurred there as competitors. The distribution of the food with respect to cover and covey territories is of infinitely greater significance than sheer quantity. Tremendous quantities of food may exist in the fields of a given farm, but in places available to few if any bob-whites.

A certain amount of food must be available to make a bob-white territory habitable, and a certain amount must be sufficiently available at all times to carry populations through winter crisis. But if the food supply is ample and available and properly distributed, further increase is not attended by a corresponding rise of environmental carrying capacity for quail. Conversely, if the food supply is far in excess of the needs of the wintering populations, it can stand considerable reduction without affecting carrying capacity.
COVER AND CARRYING CAPACITY

Food is the first essential constituent of a winter quail territory; cover is the second. The quality, distribution, and convenience of food and cover, together with the bob-whites' intolerance of crowding, probably determine in largest measure the carrying capacity of environment for the species.

Some food of adequate quality must always be available to quail in a habitable territory, for the birds cannot eat the cover. If the food supply is deficient, the birds cannot occupy a given territory in the first place, or will be forced out later; if it fails for any period exceeding a very few days, severe mortality may result. Emergency conditions are much more likely to be precipitated by lack of food than by lack of cover.

But quail losses through lack of cover, while almost never of the cataclysmic magnitude of some losses through lack of food, nevertheless constitute a steadier drain and one seemingly of greater significance in the determination of year to year population levels. Indeed, environmental carrying capacity for winter bob-whites seems basically to be a matter of cover limitations as much as anything else. The lethal character of territory number 14 was apparently due to cover deficiency, and cover may conceivably be the factor limiting carrying capacities of many non-lethal territories or those which are lethal only to the degree that they are over-populated.

Cover is of value to the bob-white chiefly as protection or concealment in case of attack by enemies. Lack of cover means vulnerability to predation, whether enemies are few or many. Cover has also a certain value as shelter during periods of wet or cold weather, or during storms, but the necessity of shelter for the bob-white is usually over-rated by the public about as much as the necessity of escape cover is under-rated.

In any discussion of the efficacy of the various cover types in affording concealment or mechanical protection to quail, the role played by weather should not be overlooked. The actual utility of many cover types hinges upon whether there is much, little, or no snow. A heavy snowfall, for example, may not only bury the principal food supply and thus make a given territory uninhabitable, but it may also bury the principal cover and make the territory uninhabitable from that standpoint as well. A heavy glaze of ice may have a profound effect upon cover, particularly upon grassy and low herbaceous types.

The adverse effect of deep snow upon adequacy of cover is especially evident when the chief cover provides better opportunities for escape by hiding than by flight. Stubble, low growths of weeds or grasses, dry leaves, hummocks, stumps, clods, or merely unevenness of terrain may serve more or less well for concealment in open winter weather, but the bob-white cannot use this sort of cover when it is buried under snow.
Dry snows reduce the concealment value of cover much more than do wet snows. In some instances, wet snows, by accumulating on the tops of marsh or heavy weedy growths, furnish such an effective broken canopy that the concealment and refuge value of the cover may even be enhanced thereby, if the vegetation does not settle too much under the added weight. Wet snow upon ordinary brushy cover (fig. 7) has an undetermined but not necessarily adverse effect upon cover value as long as it sticks to the branches; if it settles down, it detracts considerably from the utility of the brush as cover for quail; if it melts soon, as wet snows commonly do, patches of leaves or dark vegetation appear here and there, and the difficulties of quail in finding concealment are correspondingly diminished. By and large, cover is distinctly of most advantage when there is no snow (fig. 8).

Drifting snows may bury much first class brushy refuge cover and so render it as useless to quail as the concealment cover of a similarly buried stubble field. The drifting of snow is sufficiently uneven, however, that much cover is usually not affected to any serious extent, and patches of bare ground are left, notably at the bases of trees, around fence posts, and at the tops of elevations. After a time, too, holes large enough to allow passage of quail may take form about protruding branches and these may lead to roomy snow cavities within.

All in all, the effect of snow on habitability of quail environment is decidedly hard to evaluate. Seasoned birds are canny in looking out for themselves and take advantage wherever they find it, within the limits of their physical powers and adaptability. They may resort to farm buildings, holes in the ground or in snow banks, dumps, rolls of wire, scrapped auto-

Fig. 7. Wet snow upon certain types of cover may form canopies under which bobwhites may find good concealment.
Fig. 8. The efficiency of cover is usually best when there is no snow.

Bob-whites are no real sticklers for rules. They live if they can and where they can, as do other wild creatures. Like other wild creatures, they have traits and adaptations of positive, negative, or indifferent survival value. On the whole, they may be said to give very good account of themselves. They may at times exist in the face of incredible obstacles, but they cannot be expected to do it regularly.

The mere fact that quail have been known to live in a virtually coverless cornfield, or to find refuge in a woodchuck hole or a drain tile, or to escape enemies by diving into leaves or soft snow, does not alter the fact that, in the main, they must have effective brushy cover within access of wherever they may have to feed. This they must have, so far as we have been able to determine, not only if they are to thrive but if they are to exist at all.

For purposes of this bulletin, cover types may best be classified according to their mechanical qualities rather than according to the systematic position of the plants composing them. When the systematic composition of a given cover type is mentioned, it is only to aid the reader in visualizing the characteristics of the cover. Bob-whites seem to care little if a winter refuge thicket is made up of raspberry canes, plum brush, or something else, as long as it serves their needs.
Likewise, the birds care little whether man may classify their chief cover as herbaceous or brushy, but no hard and fast separation should be made here. Dense weeds and dense brush make a very effective combination (fig. 9), appreciably more effective than either weeds or brush alone.

The more bare the ground appears under winter conditions the less it provides concealment or refuge for bob-white. A closely grazed grass pasture is nearly at the bottom of the scale (foreground fig. 10); next is short-cut stubble and hay fields, golf greens, park lawns, etc. Heavy grasses, especially in relatively ungrazed low spots (fig. 11), represent choice cover for night roosting as well as for daytime concealment. Growth of sweet clover (*Melilotus* spp.), goldenrod (*Solidago* spp.),
Fig. 11. Good cover for night roosting and daytime concealment. The brush adds to the value of the grass for this purpose.

ragweeds (*Ambrosia spp.*)*, lamb's quarters (*Chenopodium spp.*)* and vegetation of this general consistency and habit (fig. 12) may offer good concealment but not too adequate mechanical protection, unless supplemented by brush as in figs. 11 and 15. Dense stands of burdock (*Arctium minor*), marsh elder

Fig. 12. Growths of goldenrod — sweet clover type — furnish better concealment facilities than mechanical protection.
Fig. 13. Open brush, as sumac, may be distinctly inferior as winter quail cover.

(Iva spp.), hemp (Cannabis sativa) and other coarse weeds may sometimes give as effective mechanical protection to quail as many of the brushy cover types.

The more open brushy cover types such as Sumac (Rhus spp.), may, in fact, be quite inferior to heavy weed growths as refuge to quail (see foreground of fig. 13). Better cover is afforded by willow (Salix spp.), osier (Cornus spp.), alder (Alnus spp.) and suckers growing from stumps of hardwood trees, though here again the value of the cover is less dependent

Fig. 14. Rather ineffectual brushy cover (compare with fig. 15).
upon its taxonomic position than upon its effectiveness in impeding pursuit by enemies. (Compare the open cover of fig. 14 with the dense mat of brush in fig. 15; in both pictures the cover is made up of about the same plant species.)

The quail cover on wooded hills shown in fig. 16 is only fair in quality, as may be said of most predominantly timber growths. The brush about the base of the hill, however, is of good cover quality and is similar to the raspberry (*Rubus* spp.) and sapling growth of fig. 17. The mixed stand of trees and brush illustrated by fig. 18 constitutes superior deciduous cover of a type frequently found around the edges of woodlots and in localities where the practice of over-grazing is not prevalent.

Roadside brush (fig. 19) may be of extreme utility to quail if of sufficient thickness. In this picture, the growth is largely
Fig. 17. Cover of good quality (a mixture of saplings and raspberry canes) fringing hill.

raspberry with some grapevine (*Vitis* *spp.*). The dark clump to the upper left of the picture represents a fine stand of leafy oak (*Quercus* *spp.*) suckers. Roadside brush has the disadvantage of drawing quail to places where they may be potshot from automobiles, and it is rarely safe from destruction by man.

Fig. 18. Superior deciduous cover of the type found about the edges of ungrazed woodlots.
Fig. 19. Roadside brush constituting effective quail cover. This growth is made up largely of raspberry canes and grapevine.

for any period of time. Thickets of haw (Crataegus spp.), plum (Prunus spp.), and mixed vegetation of many kinds (fig. 20) may add greatly to the habitability of a given quail territory. Massive tangles of vines not too far from the ground are notably desirable as escape cover.

Fencerow growths of grapevine mixed with other vegeta-

Fig. 20. A roadside thicket valuable to wintering bob-whites.
tion have proved to be highly superior cover on many of our
observational areas. Scraggly fencerow growths, of course,
occur and are worth little or nothing as cover, but a substantial
tangle of years' standing may be a bulwark of protection for a
covey which has no other place of refuge. Fencerow growths
seem not so likely to be disturbed as roadside growths, and for
that reason may be of superior value.

One of the best cover types of all is sometimes found in
communities in which most of the other cover has been grazed
off, i.e., the mats of creeping juniper (*Juniperus communis*
*depressa*), conspicuous in non-glaciated south-western Wis-
cconsin (fig. 21). It is commonly mixed with red cedar (*Juniperus virginiana*, a plant likewise resistant to grazing but
one of less value from the standpoint of quail cover) and often
redeems a given tract of land from utter hopelessness as quail
environment. Dense mats of creeping juniper made up the
principal cover of territory number 29.

Brush piles, if roomy inside and of fair size, furnish
exceptionally good escape facilities and greatly enhance the
value for quail of almost any cover vegetation. They may be
especially effective if carefully constructed for the specific
purpose of providing quail cover at strategic places (fig. 22).
Brush piles which have settled flat through decay may be of
scant use to desperate bob-whites.

RELATION OF CARRYING CAPACITY AND COVER

In the construction of the cover relationships map of the
Class One to Three Prairie du Sac territories (fig. 23), an
Fig. 22. Artificially constructed brush-piles at strategic situations may often hold quail coveys in places that otherwise would not be occupied. Brush-piles are recommended for over-pastured woodlots.

enlargement taken from a U. S. Geological Survey folio was used as a base, and the cover types were filled in from the field with as much detail and accuracy as time and lack of skill and instruments permitted. The map has its crudities, but it should give a fair idea of the general physiographic features of the area, the juxtaposition of usual feeding ground (cultivated land) and possible escape or concealment cover and the relative proportions of cover types to each other.

While the map represents specifically the cover conditions as they existed during the winter of 1934-35, it also depicts fairly well the conditions for all other winters back to 1929-30, with the exception of the winter of 1933-34, when all of the roadside brush was cleaned up by the CWA. The food conditions have not shown the comparative year to year constancy that the cover conditions have, although broadly the same tracts of land have been cultivated year after year. On the whole—barring drouth, snow, or fall plowing—the food conditions on the various territories have not shown much change during the six winters of intensive observation.

After scrutiny of the map (fig. 23), we must confess that we fail to see much correlation between limits of carrying capacity and the gross quantity, quality and distribution of the cover.
CARRYING CAPACITY
Of Territories on the Basis of
Median Survival 1928-1935

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<th>TERRITORIES</th>
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<tr>
<td>#7</td>
<td>59</td>
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<td>#14 (Lethal)</td>
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Fig. 23.
We know, at one extreme, that quail may winter in corn shocks or even in rather open fields. We know that some consistently quail-vacant or lethal territories may have more cover than some of proven habitability. We know that artificial improvement of cover may not necessarily raise carrying capacity, and we know that a great deal of debrushing and "cleaning up" may not necessarily lower carrying capacity.

We do know, on the other hand, that carrying capacity has been both raised and lowered by changes in cover conditions. Environmental manipulation, for one purpose or another, may often be of profound consequence to bob-white populations, but we see no way of predicting its effect in advance. To be sure, we may predict with reasonable certainty that a strong spread of fencerow and roadside brush in central Iowa may be followed by an increase of quail and that any wholesale reduction of existing cover would probably mean decidedly fewer quail, but there is a great deal about this that we do not know, especially as to details.

Leads as good as any perhaps may be given by the data from territories number 11, number 17 and others where relatively slight environmental modifications have made territories unattractive, if not lethal. The cleaning out of one small but strategically located patch of roadside growth apparently changed number 13 from a habitable to a lethal territory. The burning of a single brush-pile, likewise strategically located, patently left territory number 11 with an altered status, so far as wintering quail were concerned.

From data of this sort as well as from the stability of carrying capacity so frequently maintained by bob-white territories despite changes in the cover equation, we may be tempted to conclude that only the cover in certain portions of a territory may be significant. In a number of instances, territories have been studied in some detail with reference to the daily routine of resident coveys, but so far there seems to be nothing which habitable territories may be said to have in common except food and cover sufficient for the rather variable needs or preferences of the birds. A territory simply seems to be adequate if the birds like it and can live there, whatever may be its score when judged by human standards.

We may go a bit further and postulate that the instinctive reactions of the quail themselves to the "lay of the land" in times of sudden crisis may be a partial answer. It is quite conceivable that certain coverts may have strategic importance to the bob-whites, not so much because of any singular qualities which they may have as coverts, but because the quail may for some reason tend to use them. It is conceivable also that strategic coverts may be inferior both in quality and in accessi-
bility to non-strategic coverts but may be strategic solely because they may be the ones used when the quail are hard pressed by enemies.

The detailed determination of what constitutes habitability for wintering bob-whites does not present the theoretical difficulties offered by the determination of what governs definiteness of carrying capacity, still assuming that such a thing exists. We may, in the not too distant future, be able to evaluate the constituents of an environment and say with reasonable certainty that it is or is not habitable for quail; but whether we may ultimately, without survival records, be able to tell within a bird or two what is the carrying capacity of a given territory is another matter.

Stoddard (letter, Aug. 27, 1935) feels that the time required for quail to fill their crops is of vital importance, especially when snow is on the ground. He considers quail most vulnerable to accipitrine hawks while feeding. This is doubtless true, but probably greater winter losses from predation are suffered by northern quail at hours when they are not feeding, notably at night.

One of the greatest obstacles in the way of theoretical explanation of definiteness of carrying capacity is the fact that the predation which reduces the surplus is of several different types. If the predation were due entirely to foxes, or entirely to Cooper's hawks or entirely to something else, some sort of plausible hypothesis might take form. But these predators all have more or less different hunting techniques, yet their net collective effect seems to be about the same; in the absence or scarcity of some important predatory species, the pressure of others seems to compensate. Why should only about so many bob-whites be able to survive in a given territory, seemingly irrespective of the kinds and numbers of predators?

Difficult as it ordinarily is to trace a substantial proportion of quail kills to specific predators, it is still more difficult to witness the actual killing or to reconstruct with satisfactory accuracy and completeness the story of the event. Data of this sort trickle in with extreme slowness, but they do come, nevertheless; and in the aggregate, over a period of years, partially answer some questions and raise a great many more.

From the data we have, it seems that foxes usually get winter bob-whites when individuals are separated from the covey and are hiding singly, either on the ground or in tufts of grass. Cooper's hawks may catch birds by surprise while they are on the ground or overtake them if they have too far to fly to suitable cover. If the refuge cover is inadequate, the pursuing Cooper's hawk may follow its prospective victim on foot. Marsh hawks make captures by flying low over fields and suddenly dropping on birds which they may find practically within reach when visibility is poor. Horned owls, in the main,
seem to get birds that are wandering about in the dark, and especially those that have been night-flushed to alight in exposed places, such as snow covered open hillsides. How less efficient predators get healthy adult winter bob-whites, except through cornering them by chance, we do not know. When the birds are from some cause too weak to fly, there is less mystery about how they may be caught by any predator, whether of regularly formidable or commonly inconsequential type.

There doesn’t seem to be anything of exact similarity in the hunting tactics of any of the principal types of predators. Still, the net result of the pressure of all of these seems not to differ materially from the net result of the pressure of any one in the absence of the others, although they are not all capable of reducing quail surpluses with uniform rapidity. For example, it might take most of the winter for foxes to reduce a given overpopulation which Cooper’s hawks could consume in a week or two.

The role of education in determining the reaction of quail to predators is not as clear as it might be. There is some reason to believe that some of the early winter losses may be due not so much to over-population as to unwariness of some of the birds, possibly the younger ones. It is quite apparent that sometimes a lesson—such as the loss of a member of the covey to the supremely dreaded Cooper’s hawk [Errington (13)]—may be needed to put a covey on guard, and the lesson may be needed in mid-winter as well as in the fall. The data which we have indicate that secure bob-white coveys will not suffer appreciably more from a moderate wintering population of Cooper’s hawks than from perhaps a single individual drifting through in the course of the winter. All in all, we are inclined to include the “educational” winter losses with the immaterial 5 or 6 percent previously discussed rather than with the losses through over-population, which concern us mainly.

But for all of the heterogeneity of the predation data, one thing does seem to make a certain amount of sense: An extensive, dense, thicket tangle adjacent to an adequate and convenient food supply is an excellent all-around protection from enemies collectively. Even so, the strongest natural coverts, artificially strengthened further by sizable brush piles with grain within, seemingly have a limitation of carrying capacity far below the actual feeding and refuge facilities they make available to wintering bob-whites.

**TERRITORY AND CARRYING CAPACITY**

We shall make no effort in this writing to review the literature dealing with the natural means by which animal populations are held in some sort of check. It is evident enough that no species may actually continue to increase year after year
indefinitely and bring young to maturity at rates comparable to its theoretical reproductive potential.

Elton (10) in critically discussing the “balance of nature” concept says, “Now, I suppose the picture of the internal arrangements of an animal community that is most frequently drawn for us is one in which the powerful tendency to increase in numbers which is possessed by every species is exactly cancelled out by some effective controlling factor—for many animals their enemies, for others also the climate, food supply, breeding places, and so on . . . . . it is assumed that an undisturbed natural animal community lives in a certain harmony, referred to as ‘the balance of nature’, and that although rhythmical changes may take place in this balance, yet that these are regular and essentially predictable, and, above all, nicely fitted into the environmental stresses without.”

He continues, “The picture has the advantage of being an intelligible and apparently logical result of natural selection in producing the best possible world for each species. It has the disadvantage of being untrue. ‘The balance of nature’ does not exist, and perhaps never has existed. The numbers of wild animals are constantly varying to a greater or less extent, and the variations are usually irregular in period and always irregular in amplitude.”

Nevertheless, while the “balance of nature” may not be everything it has been thought to be, the fact should not be overlooked that biotic equilibria of some sorts do exist. For example, Chapman (5 p. 188) has experimentally demonstrated for the flour beetle (Tribolium confusum) that, “after a period of approximately 100 days, the number of individuals, as expressed in beetles per gram of flour, becomes constant at about 43.97 individuals per gram and fluctuates about this number.” He found that there were wide fluctuations in egg numbers but not of adult populations and that cannibalism was the mechanism of control. “At low concentrations, eggs and pupae escape and develop to become adults. When many of them have developed into adult beetles, the concentration is then so high that relatively few eggs or pupae are able to escape; and the population then remains constant.”

[For further discussion on the general topic of animal population limits the reader is referred to Allee (1).]

Howard’s (42) work on territorial relations of nesting birds, mainly passerines, has probably done as much as anything to open up a new field of thought and to stimulate research on the role of territorialism in vertebrate ecology. At the present time, a great but rather belated interest in this phase of bird study has been manifest. Nice (62) states, “The recognition of territory in bird life has been epochal in its effect on students of the biology of birds; the science of life history study has
been reoriented thereby in the last dozen years.” Nice (63,64, 65, 66) through her studies of the song sparrow (Melospiza melodia) has contributed materially to the science in this country and has significantly reviewed the literature on the subject (62).

And, although Nice (62) cautions that “the latter [the bird students of the world] are in danger of going territory-mad,” it is evident enough that the ecological exploration of the field has barely begun. The concept of “home range” for vertebrate species is now anything but new, but what does it signify, what is its importance in the determination of population levels?

A partial answer is expressed by Nicholson (67): “When animals lay claim to territories . . . . it is clear that in any given area there is room for only a limited number of territories. Consequently, the surplus individuals are continually harried by their more fortunate brethren, or are forced into unsuitable environments, and so their chance of survival, and of producing offspring, is greatly reduced. The system of balance resembles that of water in an overflowing reservoir . . . .”

Nice (62), endeavoring to discourage loose usage of the term “territory,” says in the summary, “Territory implies in the male bird isolation, advertisement, fixation, and intolerance. Where these four aspects are not present, the bird does not truly hold territory . . . . It may be that the food aspect of territory has been over-emphasized, and that sex jealousy in many cases plays a definite part.”

It is rather evident at this time that the role of food in governing animal population levels generally has been and is still very imperfectly understood, and certainly has not the precise general importance formerly attached to it by many naturalists of the Malthusian school. McAtee (60) in particular points out that relatively few organisms increase up to the limit of their food supply, save under exceptional conditions.

That territorial intolerance, or at any rate, over-crowding, may have manifestations not explainable by present knowledge is surely to be expected. There seem to be, among other things, psychic or physiological inhibitions which serve to slow breeding rates as populations approach saturation densities.

Kendeigh (44) believes, for the house wren (Troglodytes aedon) in Ohio, that “the number of broods per female per season tends to vary inversely with the total population”; also “This compensating reproductive resilience may not become effective the same year as a major calamity . . . .” Nice (letter Aug. 22, 1935) is not sure of this point, however, and states further regarding her own specialty, another small passerine bird, the song sparrow: “Although the population on Interpont has varied in the past six to seven years between 33 and 87 pairs, the average number of eggs laid in a set has barely varied at all.”
R. T. King (unpublished) has observed at Cloquet, Minn., that the size of ruffed grouse (*Bonasa umbellus*) egg clutches diminishes with rise of population density during the upgrade of the cycle.11

Up to date, the vast preponderance of literature on vertebrate territorialism has dealt with population relationships during the breeding season. The term "territory" has all but come to have an accepted meaning of breeding territory among ornithologists, but we see no valid reason why the usage should be so restricted.

There is an evident fixity of range found in some non-breeding populations outside of the breeding season; there are on such ranges individuals or groups of individuals which are at least to some degree isolated and to some degree intolerant of other individuals or groups; and, while there may not be conspicuous advertisement such as occurs in the breeding season, the residents may not be hesitant about making their presence known to trespassers from the outside.

In the case of the bob-white, the birds seem to have an awareness of when their winter territories become over-populated, either with their own species or with mixtures of their own species and others as the ring-necked pheasant. Apart from direct predation, the chief mechanism by which over-populations are reduced in a given area seems to be that of departure of the surplus birds. Much of the departure—especially during the winter months—seems to be voluntary, but the indications are that strife between fall coveys [Errington (24) and unpublished] may have a role in the establishment of winter territories.

It is, of course, true that the fighting between coveys in the fall may be the natural outcome of the meeting of strangers and may be an early stage in the establishment of a pecking order. A certain amount of friction occurs within wild coveys through the winter, which, with the other evidence, may suggest inequalities in the social scale. One observes apparent outcasts now and then, or at any rate single birds in strong condition which have stationed themselves near but apart from roosting or resting covey groups. Are these single birds strangers, unpopular individuals, or some simply unable to look after their own interests, or undesirous of too close intimacy with the others?

We cannot say whether the frequent adjustment of covey

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11. The phenomenon of cyclic or periodic fluctuations of animal populations is of extreme importance biologically. It effects conspicuously populations of rodents, rabbits and grouse in northern regions, but neither its causes nor its influences are well known. There is some evidence that the bob-white, among other species, may be subject to periodic as well as irregular fluctuations, though this as yet has been investigated too imperfectly to justify much opinion. For literature on animal cycles the reader is referred to Elton (8, 9, 10), Leopold (48), Green and Schillinger (39), Severtzoff (69), Wing (77), Matamek Conference on Biological Cycles (61).
numbers to conform to the carrying capacity of the wintering territory is precipitated by predator pressure from the outside, though not necessarily pressure of sufficient intensity to be lethal before adjustment occurs.

The strongest probability is that consciousness of crowding plays an important part in the general distribution of the quail population in the wintering territories, but that the specific self-adjustment of covey numbers to the carrying capacity of environments with such frequent exactness is forced. If it were due only to a vague uneasiness on the part of the covey as a whole that too many birds were present, one might expect some birds of the covey to split off and leave. If it were due only to a feeling on the part of dominant birds in the covey that the covey should not exceed a certain size, they could conceivably keep it from exceeding that size by punishing out the excess. But the fact that carrying capacity seems to have such a definite value, season after season, and that mortality follows over-population of even minor degree, is far from being explained entirely in terms of species behavior, or territorialism. That these have influence in the winter equation, however, seems quite evident.

BIOLOGICAL APPLICATION OF POPULATION VULNERABILITY

In the first place, we may admit that we do not know what is responsible for the definiteness of environmental carrying capacity noted for wintering bob-white. We are not so sure that carrying capacity is such a definite thing as the present data indicate, or that a population entrenched with ordinary security in an environment would be secure against all natural enemies with which it could conceivably be confronted.

Armed and ingenious man has often demonstrated his ability to reduce populations that live in comparative security from other directly predatory enemies. Man may be supremely efficient as a predator when he wants to be, in which respect he cannot even be approached by wild predators. Stoddard (letter, Oct. 4, 1933) thinks that Cooper’s hawks may still get quail when they are safe from about everything else, and also that the goshawk (Astrur atricapillus) may be a still more formidable enemy on the occasions of its infrequent visitations from the north. In our studies, we have never personally had the opportunity to witness the work of goshawks upon quail, and the pertinent data we have are second hand [Errington (19)]. The goshawk, however, may be looked upon as a sort of super-Cooper’s hawk (the female Cooper’s hawk almost equals the male goshawk in size), and surely any superiority of its prowess is only one of degree.

But whether carrying capacity of specific bob-white winter
environment is really definite or not, populations exist which are so securely situated that even modern man has difficulty in taking much of a toll by direct pressure, even in the course of long hunting seasons. We have known Cooper’s hawks to harass certain well situated coveys for weeks at a stretch without getting any of their members, or getting at the most a very few birds in the course of the winter.

McAtee has recently restated his thesis that predation tends to be in proportion to population (56) to the effect that the proportion, however, rises and falls progressively with the increase or decrease in numbers of the available food organisms (58). Errington (31), for reasons evident from the bob-white studies, suggests that predation may be in some cases proportional to over-population instead of to population; he also raises the question if many animal populations may not in analysis be composed of vulnerable over-populations and secure residua, which residua, nevertheless, may not necessarily be insignificant numerically.

Indeed, it seems as if any number of species may live in relative security from predators at given population levels in given habitats. Errington (MS accepted by Canadian Field Naturalist, 1935) presents some evidence that very low populations of ruffed grouse in marginal environment may be thus maintained with little change during the winter months, though Gardiner Bump (letter, July 15, 1935), from investigations in good ruffed grouse country, writes: “All in all, I do not feel that in New York adult grouse populations within the carrying capacity of the range exhibit any significant security of position.” On the basis of unpublished and fragmentary local evidence, we suspect that the muskrat (Ondatra zibethica) may also belong in this category, at least under some circumstances.

Tinbergen (75), studying the food habits of the Waldoreule (Asio o. otus) and the pressure of this owl upon Microtus arvalis, concludes that the control of mouse populations by predation is most effective at what we understand to be moderate levels; rises of prey populations toward top-heavy peaks plainly get out of control.

Gause (36) quotes Kalabuchov and Raewski on observations made in the North Caucasus: “The picture of the destruction of mice by different predators is a curious one. At the beginning of the destruction about the same number of rodents is devoured daily. But as the density of rodents diminishes it becomes more and more difficult to catch them, and the number of mice devoured gradually decreases. Finally a time comes when the relation between the density of the rodents, the presence of cover or refuge (burrows, vegetation, etc.) and the biological peculiarities of the predators become such that the latter can devour the rodents only in rare cases. In this way the number of the rodents remains constant.”
This represents population vulnerability of a staple prey species rather than an incidental prey species as the bob-white. Species in one category seem to be characterized by secure residua that may be very small compared to the population levels commonly reached and, at the same time, characterized by comparatively tremendous over-populations of vulnerable individuals. At the other extreme, we may have species usually characterized by large secure residua and small or negligible over-populations. From one extreme to the other, we may expect that some entire animal populations as they may occur in nature—particularly as adults—may consist almost wholly of over-populations or almost wholly of secure residua, with all intermediate gradations. Whether or not the numerical tendency of a strong species is toward habitual over-populations, or towards levels of greater stability, seems to depend upon how strictly its increase may be controlled by limitations of environment.

We do not imply that population vulnerability has universal biological application. We do not know what may be its application. It is apparent, however, that all vertebrate species are not wholly vulnerable in the same way or at the same stages of their life histories. We are not in the least sure that all species have secure residua at any population level, high or low.

That population vulnerability may to some extent apply to avian nests and young more than to adult populations is indicated by recent wild duck breeding studies carried on by Iowa State College staff members in north-western Iowa, chiefly by Logan J. Bennett. Our experience has been that most of the duck nests exposed on account of human meddling, mowing, close grazing, insufficient natural cover, precarious locations, etc., were likely to be destroyed, irrespective of the presence of particular predators, including the highly unpopular crow (Corvus brachyrhynchos).

"Similarly, we suspect from limited observations that crow depredations upon ducklings may be largely linked with exposure. It is not surprising that many instances have been reported from drouth regions. Small ducklings forced into shrinking puddles with yards of sticky mud between them and the nearest cover are truly in a bad way. Crows may get them or marsh haws [may] or other flesh eaters, or they may mire down or die of thirst . . . Depredations may be more correctly a matter of how many ducklings are ready to be picked off rather than one of few crows or many crows . . . The basic principle underlying predation is availability of prey“ [Errington and Bennett (34)].

Logan Bennett (6), comparing two duck nesting seasons in the vicinity of Ruthven, Iowa, estimated that in 1934 over-
grazing and drouth destroyed 75 percent of the nesting cover on lands where the nesting conditions had been excellent in 1933. In 1933, only 15.3 percent of 137 nests were total failures; in 1934, 64 percent of 103 nests were lost from all causes, including enemies which found the ill-concealed nests much more available.

Nice (letter, Aug. 27, 1935) writes regarding song sparrow populations “... during the first two years on Interpont the survival of the birds was splendid—over 60 percent with the males, but now that it has been destroyed, the survival has fallen as low as 23 percent. Apparently the birds will take up these territories that prove lethal to them—partly through attachment to a former territory, even when considerably changed, partly probably because there is so little really good song sparrow territory anywhere in the vicinity.” [See Nice (66) for a more detailed discussion.]

In short, while it is not always easy or even possible to distinguish with exactness between mortality due to predators or due primarily to something else, it is apparent that no predator will prey upon an animal which it is unable to get, whatever may be the precise reasons for its inability to do so.

PART IV. MANAGEMENT OF THE BOB-WHITE’S WINTER TERRITORY

MANAGEMENT AND ITS OBJECTIVES

“Wildlife management” implies a less passive technique than the older term, “conservation.” It lays more emphasis upon the improvement and maintenance in an improved condition of environment for wild species and less emphasis upon legal protection and the establishment of sanctuaries. As the term is used here, management does not mean artificial propagation. It means the encouragement of wild species under conditions as nearly natural as possible. Management is applied ecology. It is human manipulation of wild populations and may be motivated by economic, aesthetic, or scientific objectives.

From the beginning of settlement in North America, the white man has manipulated wild populations, though not always consciously or always with definite intent. His agricultural and commercial practices and exploitation of available resources have profoundly altered the habitats and the numerical status of the wild species which he found here. The mere fact that many of man’s manipulations have been blind does not lessen their ecological significance, nor does the fact that man may not be qualified to judge what is to his interests, or that his interests may be narrow, selfish, or shortsighted.

Man will unquestionably continue to manipulate for his own ends his own environment and that of other living creatures.
His manipulations may be conservative, as befits those of a thinking being, or they may be little more than meddling with mechanisms which he neither recognizes nor appreciates. His own destiny is dependent to no slight degree upon how he manipulates.

To quote from Leopold (48) on the social significance of game management: "The game manager manipulates animals and vegetation to produce a game crop. This, however, is only a superficial indication of his social significance. What he really labors for is to bring about a new attitude toward the land.

"The economic determinist regards the land as a food factory. Though he sings 'America' with patriotic gusto, he concedes any factory the right to be as ugly as need be, provided only that it be efficient.

"There is another faction which regards economic productivity as an unpleasant necessity, to be kept, like a kitchen, out of sight. Any encroachment on the 'parlor' of scenic beauty is quickly resented, sometimes in the name of conservation.

"There is a third, and still smaller, minority with which game management, by its very essence, is inevitably aligned. It denies that kitchens or factories need be ugly, or farms lifeless, in order to be efficient.

"That ugliness which the first faction welcomes as the inevitable concomitant of progress, and which the second regretfully accepts as a necessary compromise, the third rejects as the clumsy result of poor technique, bunglingly applied by a human community which is morally and intellectually unequal to the consequences of its own success."

That the necessity for a more harmonious relationship between man and his environment is no longer something to concern only the aesthete should be apparent from the evergrowing menace of soil erosion. H. H. Bennett's (2, 3), Darling's (7) and Taylor's (74) writings are fraught with ominous meaning, and the lesson may hardly be missed that the wages of continued waste are ruin.

Leopold (49) warns that "Civilization is not . . . . the enslavement of a stable and constant earth. It is a state of mutual and interdependent cooperation between human animals, other animals, plants, and soils, which may be disrupted at any moment by the failure of any of them. Land-despoliation has evicted nations, and can on occasion do it again . . . . It thus becomes a matter of some importance, at least to ourselves, that our dominion once gained, be self-perpetuating rather than self-destructive."

At once an indictment and a prayer, we find the concluding paragraph of Leopold's admirable pioneering text on game management (48, p. 423):

"In short, twenty centuries of 'progress' have brought the average citizen a vote, a national anthem, a Ford, a bank
account, and a high opinion of himself, but not the capacity to live in high density without befouling and denuding his environment, nor a conviction that such capacity, rather than such density, is the true test of whether he is civilized. The practice of game management may be one of the means of developing a culture which will meet this test."

It is the integration of human ends that game management—or more broadly, wildlife management—implies which bears social promise. Management, to have the fullest social promise, must mean more than the taking of what is to be taken; it must mean a closer real harmony between man and land, between man and other living creatures of the land. Management must be socially and biologically self-sustaining, for, governed by any standards other than those of permanence, it becomes only exploitation, whatever it may be called. And the handwriting on the wall should be clear enough at this time to tell us that we as a nation or as a species have had about enough of exploitation.

INTEGRATION OF ENDS IN LAND USE

Leopold writes (51): “... For the last half century there has grown up a widespread conviction that our whip-hand over nature is no unmixed blessing. We have gained an easier living, but in the process of getting it we are losing two things of possibly equal value: (1) The permanence of the resources whence come our bread and butter. (2) The opportunity of personal contact with natural beauty.

“Conservation is the effort to so use the whip that these two losses will be minimized.”

Leopold, in the same writing briefly analyzes from the standpoint of conservation economics the problem of wise land use. He stresses the need of comprehensive fusion of interests and sweeping simplification of conservation law, with the single criterion of land use: “Has the public interest in all its resources been protected?”

No longer may destructive private land use be condoned on the grounds that a man’s land belongs to him and that he has a right to do with it exactly as he pleases, whatever that may be; and that whatever he does with it is his and no one else’s business. But although the social consequences of land abuse become increasingly apparent to thinking people, and the necessity for integration of human ends gains recognition, the means of integrating those ends is still to take form.

We do not presume that the answer to the ills of mankind is anything as simple as the management of the bob-white quail. The management of the bob-white, however, may be closely linked with wise use of the land.

The bob-white thrives best in agricultural communities, and
its fortunes in the long run are essentially the fortunes of the soil. Bob-white management may be to a large degree correlated with erosion control. Management of this, as well as other wild species of similar requirements, may reasonably be dove-tailed into sound agricultural practice over wide areas of land. In the overwhelming majority of instances, management of the bob-white may never be more than incidental to good land use, but we fail to see why it should not be carried on incidentally. Bob-white management, properly conducted, at least need not be detrimental to permanent agriculture.

To the question, "Why manage bob-white?" perhaps the best answer is another question, "Why not?"

There are many farm customs which could be modified in behalf of the bob-white, and the chief modification often need cost little or nothing in time, labor, money, or efficiency. A great deal in management may be accomplished merely by headwork, by remembering that living creatures cannot continue to live without a place to stay and something to eat. Simplicity characterizes some of the measures that may be quite effective in less intensive grades of management.

The more intensive the management is intended to be, or the less suitable is the area to be managed for bob-white, the more difficult the management may become. In the event that an area is to be managed to produce the maximum number of birds for shooting purposes, field trials, etc., management may become more complex and more expensive.

But the farmer who just likes to have the birds around need not go to much trouble to insure the permanence of a covey or two which he may have on his farm, or perhaps to establish a new covey in some covert not previously occupied.

After all, perhaps the strongest argument for the preservation of wildlife—not solely shootable game, but all native species that can be made to fit into our economic and social system—is the enjoyment that may be derived from their presence, whether their presence may be of more material benefit or not. Anything which provides a healthful diversion from the monotonies and worries and accelerated pace of modern life surely has a social value which should not be overlooked.

Finally, effective bob-white management is not necessarily a matter of what is done; more often it seems to be a matter of what is not done. The truth and significance of this thought may possibly be more readily appreciated when one considers that, of the usual practices which evict quail populations from many farms, not a few are practices which work to evict human populations, ultimately and permanently, from the same land.
MANAGEMENT OF BOB-WHITE FOOD

Liebig's Law of Minimum, as restated by Taylor (73) has application to the management of the bob-white conspicuously when one considers it from the standpoint of food: "The growth and functioning of an organism is dependent upon the amount of the essential environmental factor presented to it in minimal quantity during the most critical year or years of a climatic cycle."

This is illustrated for bob-white by the profound effects of killing winters on the population levels of the species over wide areas in the northern fringes of its range. In some localities there is starvation mortality nearly every winter, and populations rarely have a chance to attain levels which the environment could securely accommodate otherwise. Sometimes, as in central Minnesota and central Wisconsin, a succession of open winters permits tremendous increase of bob-whites [Leopold's "irruptions" (48) pp. 50, 58-64]; then, a season of heavy snows comes and the quail are gone again.

The likelihood of cataclysmic starvation emergencies diminishes with more southerly latitudes, although irregular emergencies still decimate populations as far south as Missouri. There is practically no locality in the north-central states where starvation losses on unmanaged areas may not be expected to recur with varying frequency.

It has been pointed out before that, while winter feeding of bob-whites bears more promise as a management measure to insure the security of wintering populations rather than to raise the carrying capacity of the land, it makes whatever carrying capacity there is more fully available.

There is one thing that the provision of food for a rather unexpected emergency and for the regular use of an entire bob-white population should have in common. In either case, the feeding should be adequate for all the birds that need it as long as they need it. This may not be at all or perhaps but 1 week of the winter in an agricultural community; it may be 6 solid months on wild lands or on lands reverted or withdrawn from agriculture. The feeding program should always be planned so that whole populations may be taken over "on relief," so to speak, for periods during which, for emergency or other reasons, the carrying capacity of the land for quail may be suspended.

The difference in principle between providing food for emergency or regular use lies in the stress that should or should not be placed upon making the supply attractive. If man, on wild or reverted lands, expects by artificial feeding to maintain populations at levels found on cultivated lands, he must furnish a satisfactory substitute for the waste grains and edible weed
seeds that are available incidental to cultivation. Unless he does this, he will have at best a sparse population after the "fall shuffle" and one that he may by no means feel certain of holding if there are cultivated lands adjoining.

On the other hand, if a great part of the management problem is not to hold the birds in a given territory in the first place, but to insure their security in the event of emergencies, it might be advantageous not to make the artificially supplied food too attractive. The ideal food for such a purpose would be one which the birds would not relish to the extent that they would neglect the foods naturally available, and so clean up the emergency food before it was most needed, yet it should be one capable of sustaining life during severe winter weather. The ideal emergency food should also be one which would not be likely to be cleaned up early in the season by competing forms, i.e., small birds, rabbits, squirrels, pheasants, livestock, etc. Whether such an ideal food exists we do not know. At any rate, we have never discovered it.

Corn, for general purposes, seems to constitute the best all around winter quail food in northern states. It may or may not be eaten as a regular staple, but even when the birds show a preference for some other food, as the achenes of lesser ragweed, they readily turn to corn during crises. Adult birds have no difficulty in swallowing the kernels and learn even to shear away the husks to get at the ears (fig. 24).

Corn is best made available in partly open shocks strategically placed with reference to suitable cover, or left unpicked in a few rows at the edge of a field. Squirrels and rabbits may compete severely with quail for a limited supply, but this competition may not have an entirely adverse effect. Rabbits frequently make corn available to quail after ice storms by biting through the ice glaze on the ears. Squirrels often drop quantities of kernels (with embryos eaten) at the bases of trees, where they may be found by appreciative birds. Some coveys may even make a round of the squirrel trees as a part of their daily routine, and we have known coveys to depend for food upon the corn and acorn fragments shelled out by squirrels.

Some types of feed hoppers work quite satisfactorily, especially those of simple design and those not requiring much human attention, and especially those inside of or surrounded by large loose brush piles. The efficacy of a feeding station depends largely upon where it is placed and upon how functional it may remain for weeks at a stretch when no one can or cares to get around to look at it.

The utility of food patches planted and left unharvested for quail and other wildlife varies with the circumstances. Food patches have been known to work and they have been known not to. Our present opinion is that food patches on non-agri-
cultural land should be of fair size (up to a half acre or an acre) and should be long and somewhat narrow rather than square in shape. The sizes we recommend are larger than those usually planted, but they should be large enough to be attractive to quail as well as large enough to feed the rabbit, rodent and miscellaneous competitors which are usually present.

For use in food patches we have found sorghum, kaffir corn, buckwheat, and soybeans fairly satisfactory but not outstandingly so. A considerable amount of interesting experimentation is in progress in a number of states, and there is a growing literature upon the subject, but anything more than very tentative conclusions would be premature at this time.

In simplest practice, assuming that there were no valid objections, farmers might well leave unplowed until spring the sides of stubble fields grown up to pigeon grass and lesser ragweed, and so give the birds a chance to feed on the seeds during the winter. During deep-snow crises, grain-bearing manure might be scattered on fields nearest brushy borders instead of far out toward the centers. If the farmer’s habit is to haul his shocked corn in from the fields about as he needs it for winter stock feeding, he could with practically no trouble leave for the last those shocks which were situated near quail coverts. He might not even be inconvenienced or out of pocket if he deliberately left out a few shocks for the quail until winter was safely over.

Where deep and lasting snow is expected each winter, each
bob-white covey should have access to partly open corn shocks or to a number of sources of substantial foods equally dependable throughout any ice or snow storms within probability. Shocks properly constructed furnish emergency refuge as well as food, and if the food becomes exhausted or too difficult of access, additional grain may be thrown inside now and then.

This should be emphasized: Any method of feeding which demands daily human attention or forces the birds to feed in one place is intrinsically unsound. The more automatically the food remains available and the more alternative courses of action the quail have in the event of visitations by predators, the more security may be assured.

Although the food in a given locality may be roughly adequate during ordinary winters, ice storms and deep snows may precipitate wildlife crises that call for large scale action. Broadcasting of grain on top of the sleet or snow is an excellent emergency measure but not one to be recommended for steady feeding because of its wastefulness and because of the irregularity with which food may be put out. On the whole, it is much easier to induce people to get out on occasion with bags of grain than to inculcate into them the idea of planned management. Repeated radio broadcasts and newspaper releases after blizzards may be notably effective in arousing interest; and, wasteful both of food and of energy as much emergency feeding may be, by this means great numbers of birds may often be saved from starvation.

MANAGEMENT OF COVER

Bob-white winter cover may be anything that affords the birds concealment or refuge from danger. It is usually living vegetation of brushy types or dry vegetation of herbaceous types. To be effective it must be situated within convenient distance of roosting or feeding grounds (fig. 25).

A given acreage of cover may serve the maximum number of quail if it is distributed over a farm in strips or patches rather than centralized in a solid block such as a woodlot. Occasional thickets and fencerow brush distributed here and there may constitute adequate escape cover. Cover is needed not only during the winter but during the nesting season as well.

While we are mainly concerned with winter cover in this writing, it may be significant from the standpoint of management to quote the following from a popular bulletin [Errington (22)]:

“Superior nesting cover is bluegrass or Junegrass (Poa) of the preceding years growth along roadsides, wide fencerows, and in meadows and orchards. Quail beginning to lay eggs about the first of May prefer to nest in such locations, but if all
Fig. 25. Food and cover, to be of greatest utility for bob-white, should be conveniently situated with respect to each other.

of the places naturally suited to them have been spoiled by burning, mowing, or pasturing they are forced to take what cover they can get. Nests made in scanty cover or in weedy low spots are apt to be broken up or flooded. While the quail raise only one brood a season, birds unsuccessful in hatching out their clutches early will commonly renest in the cover that is most inviting at the time, usually clover and alfalfa fields which are almost sure to be mowed over before incubation has been completed. Hence the destruction of nests [and adults and young, as well] by hay mowing would be to some extent lessened if the birds had attractive nesting territory elsewhere than in the fields.

Much of the cover deficiency in established “quail country” may be directly and indirectly attributable to agricultural practices and to the widespread feeling among landholders that all wild vegetation has to be kept “cleaned up,” irrespective of what it is or where it is. Whatever may be the alleged advantages of so-called “clean farming,” it should never be overlooked that over-zealous adherence to the doctrine may lead to the irreparable ruin of much land through erosion. “Clean farming” carried on to an extreme on soils of certain types or on lands of steep gradients may mean nothing less than community suicide.

From the standpoint of the bob-white, the restoration of adequate cover may often be accomplished merely by giving wild vegetation a chance to grow up at strategic places. Wild
## RECOMMENDED GAME COVER PLANTINGS ADAPTED TO EROSION CONTROL

Prepared by Logan J. Bennett for THE IOWA FISH AND GAME COMMISSION AND THE IOWA STATE PLANNING BOARD

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### Plants

**GROUP A**

- **Black Locust**
- **Willow**
  
**GROUP B**

- **Wild Plum**
- **Sumac**
- **Prickly Ash**
- **Hazel Brush**

**GROUP C**

- **Coral Berry**

**GROUP D**

- **Raspberry**
- **Roses**

**GROUP E**

- **Wild Plum**
- **Hazel Brush**
- **Prickly Ash**

**OTHER PLANTS**

- **Wild Grape**
- **Elderberry**

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### Table: Plants and Marginal Area

<table>
<thead>
<tr>
<th>GROUP</th>
<th>PLANT</th>
<th>Plants</th>
<th>MARGINAL AREA IN YARDS*</th>
</tr>
</thead>
<tbody>
<tr>
<td>GROUP A</td>
<td>Black Locust</td>
<td>1</td>
<td>Entire Gully Plus One Yard Over Brink</td>
</tr>
<tr>
<td>GROUP A</td>
<td>Willow</td>
<td>1</td>
<td>Entire Gully Plus One Yard Over Brink</td>
</tr>
<tr>
<td>GROUP B</td>
<td>Wild Plum</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>GROUP B</td>
<td>Sumac</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>GROUP B</td>
<td>Prickly Ash</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>GROUP B</td>
<td>Hazel Brush</td>
<td>10</td>
<td>2</td>
</tr>
<tr>
<td>GROUP C</td>
<td>Coral Berry</td>
<td>20</td>
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</tr>
<tr>
<td>GROUP D</td>
<td>Raspberry</td>
<td>7</td>
<td>2</td>
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<tr>
<td>GROUP D</td>
<td>Roses</td>
<td>7</td>
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<td>Hazel Brush</td>
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</tr>
<tr>
<td>GROUP E</td>
<td>Prickly Ash</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>

* Marginal area is the distance from the brink of gully to fence that will be put in surrounding gully.

**NOTE:** To produce an ideal game covert one strip of plants (one species) from each of the above groups should be planted. They should be planted in the order given from the gully out. The above figures are approximate and the supervisor in charge of planting will use his own discretion if a certain group of plants is not available.

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Fig. 26.
vegetation may be supplemented by plantings (preferably of native species) if the land owner is so disposed and financially able.

Commonly, we have not been advocating very strongly the intensive planting of trees and shrubs for quail cover except in connection with erosion control projects (see fig. 26). Planting on any considerable scale may involve a greater expenditure of time or money than most landholders can afford for the sake of wildlife alone. But the fencing off from stock of brushy and grassy patches here and there may not be too much trouble, nor may the erection of a few brush piles where they may do the most good.

Brush piles at the edges of pastured woodlots or open timber may add a great deal to the habitability of the land for quail, and few indeed are the cover combinations that may not be bettered by the judicious placing of brush piles. Limbs which have fallen during windstorms or have been trimmed from trees cut for firewood make good material for piling. If the landowner cares to, he may prepare cover in over-grazed woodlots or those lacking underbrush by felling trees for seasoning, lopping off the lower limbs, and stacking them about the top.

The intelligent management of bob-white cover may be difficult or easy, according to the circumstances. On some farms the prospect of encouraging bob-whites may be so lacking in promise that to try anything would scarcely be worth the trouble involved, with that object alone in mind. On other farms, it is simply less trouble to have quail cover than not to have it.

Intensely cultivated farm lands tend to have too little cover for bob-white populations of high density; wild or reverted lands tend to have too much. Lands under moderate cultivation, then, may furnish more nearly optimum environment for the species. Quality and dispersion constitute the main criteria of the effectiveness of cover in bob-white range.

There seems to be no definable minimum or maximum of cover for a habitable range. Good “quail country”—as well as that which is obviously unsuitable—is usually recognizable as such by experienced observers, but at present we are quite unable to state just where habitability begins or where it leaves off. We are sure that a marginal territory is habitable when the birds have demonstrated that it is. So far as expressing habitability of an environment as an exact formula is concerned, that may be looked forward to as a possible accomplishment of the future.

In practice, a varying amount of cover management may often be interwoven into farm routine to the advantage not only of the bob-whites but of the farm as well. Wild plant growth does not necessarily represent a thing of evil simply because it
is wild. Wild brush on a given farm is frequently looked upon as evidence of a landholder's shiftlessness, but its presence may actually denote instead a superior understanding and an advanced attitude toward the land.

Not always is there real justification for the chopping away of briars or grape vines from fencerows or the clearing of odd corners. Not always is there justification for the destruction of brush along highways where drifting snow does not constitute an important problem and where the visibility is not obstructed seriously. Unless such cleaning up has an integral role in the control of dangerous weeds or insect pests, or otherwise serves some useful purpose, much of it could well be left undone. There should be places on practically every farm where wild vegetation could be left unmolested or encouraged for the sake of wild species dependent upon it for habitats, and with no actual detriment to the farm nor inconvenience to the landholder. The concealment of unsightly places such as dumps, gravel pits, rock piles, etc., by plant growths dense enough to furnish cover for wildlife could well be worked for.

Burning, when necessary, should be done with the utmost discretion and certainly not in the nesting season of the birds. Burning may be a valuable means of stimulating later plant growth [Stoddard (70, pp. 401-410), (72)], but it is immediately destructive of wildlife environment and care should be taken to prevent fire from sweeping solid areas bare of food and of cover. While blind and habitual burning of marshes and wild lands should be discouraged, it should be borne in mind that fire has its legitimate uses as well as its abuses.

Perhaps cover management on a given farm is only a matter of withdrawal of cattle from wooded hillsides unprofitable for pasturage in the first place. Cover management does not require that vigorous growths of native vegetation be dug out and replaced by imported shrubbery of no superior merit but which costs money. Cover management need not necessarily mean any revolutionary changes in land use; it may mean simply better use of the land for the purposes for which the land may be best adapted.

**PREDATOR CONTROL**

It is true that bob-white winter populations under wild conditions frequently suffer severe losses from predators. The toll from predators, however, may be separated for analysis into a number of distinct types, and these types should be considered separately if a true understanding of predation is to be gained.

Of these types, one may be characterized by the slow rate of loss which probably continues over the whole year. We have
succeeded in measuring losses of this type only for the winter months, for which season, according to present data, the losses have rarely exceeded a rate of 6 percent of the population per 90 days for observational areas of any size. This is a loss seemingly suffered by all adult bob-white populations, regardless of how strongly they may be established in their environment. We look upon this loss as unavoidable and immaterial, since it seems to correspond rather closely to the loss which one might expect from age and accident alone if there were no predators.

Winter mortality from predation of another type becomes conspicuous when large numbers of birds are weakened by starvation, wounds, or possibly by disease, and hence are unable to escape enemies which ordinarily would have difficulty in capturing them. Starving birds so weak as to be caught easily by predators usually die anyway in a day or two, and the mortality following shot wounds and sickness is anything but low. Then, too, sub-zero cold snaps kill off the weak birds on a wholesale scale, whatever may be the cause of their weakness.

We have been trying to learn whether harassment of starving birds, as by hawks, really results in any increased loss, but so far we do not know. On the basis of observations dealing with a goodly number of starving coveys, we would judge that starvation emergencies are aggravated by attacks of predators but not necessarily enough to make much difference in final survival.

Harassment appears to be followed by most severe consequences when birds are forced to concentrate about a few sources of food, localized, as for example, at artificial feeding stations. This seems especially true when the attending predators are Cooper’s hawks. Even under such circumstances, it is difficult to evaluate with accuracy the role of harassment or of local over-population in bringing about the conspicuous mortality when observed.

The third and most important type of predation on wintering bob-whites has been discussed in detail throughout this bulletin. It represents the pressure of enemies upon that part of the quail population which is vulnerable because of its insecurity of position, or, in other words, the pressure upon what is left of the annual surplus by winter. Birds in excess of the carrying capacity of the land may be in good physical condition but they lose out nevertheless through over-crowded or inferior environment. As long as there are more birds than the winter environment can accommodate, something happens to the extra ones, and, so far as we have been able to determine, regardless of the kinds and numbers of predators ordinarily present.

We admittedly know little enough about predation upon summer adults, but the evidence seems to indicate light losses from predation except in the earlier part of the season. A certain
rise in vulnerability seems to correspond to the period when
the birds are most occupied with mating and nesting, as has
been shown by contemporaneous food habits studies on foxes
[Errington (30)], great horned owls (unpublished) and some
other predators.

A fifth type of predation—that upon eggs and young—has
not been satisfactorily studied in the North from the standpoint
of its actual effect upon quail populations. To Stoddard (70)
may be credited the best work on this phase of predation that
has to our knowledge been done on the bob-white.

So far as management of the northern bob-white is con-
cerned, aggressive control of winter predators seems to be
futile, except perhaps under unusual circumstances. Grange
and McAtee (37 p. 45) state: “When control is undertaken, in-
flux of predaceous birds from other areas soon fill the vacancies.
The yearly toll taken by predators on many game farms is
almost constant, indicating that no real progress has been made
even where wholesale control is attempted.” Perhaps Cooper’s
hawks which habitually frequent quail feeding stations may
be eliminated to advantage, but our data on this point are not
too good. On the whole, heavy bob-white winter mortality from
predation appears not so much a matter of few predators or
many predators, but of how many birds are either weak them-
selves or dangerously exposed through weakness or inadequacy
of their environment.

It is conceivable that a reasonable control of the chief nest-
ing enemies of the bob-white, under given conditions, might be
worth while from the standpoint of management. Stoddard
(70, pp. 415-437) considers such predator control important in
the management of the bob-white in southern states. His find-
ings are doubtless applicable in part to northern states, though
to what extent is not apparent. Our own studies, conducted on
lands largely trapped annually for fur-bearers during the cold
weather months, have shown little need for the taking of ag-
gressive measures against egg-eating species in north-central
states.

We have reason to believe that control of nesting enemies
is no substitute for suitable nesting cover, but, if circumstances
seem to demand that predatory species be reduced, control
measures should first be undertaken against house cats and
stray dogs and possibly forms which may be overly abundant,
such as ground squirrels (“gophers”) and crows. Any taking of
fur-bearing predators as foxes, skunks, minks, raccoons and
others should be confined, as much as possible, to the winter
months when the pelts are prime and salable; in this way a re-
grettable wastage may be eliminated, and management may be
made to pay cash dividends, sometimes very substantial.

Let it be made clear that predator control is nothing that
lends itself to rule-of-thumb formulae. It may be desirable, inconsequential, or highly undesirable—all according to the circumstances and the species subject to control. In general, it is best to bear lightly upon native species, and particularly those which have low reproductive rates or are losing ground numerically, even though as yet they may not be actually rare.

Predator control as a management measure is consistently over-rated by the public, not only as it concerns quail but practically every game or “songbird” species. Most people consider it a privilege if not a duty to kill any predatory creature on sight. This attitude is not in keeping with the findings of biological science, nor can it be said to signify the highest aesthetic appreciation of the out-of-doors and what it represents.

It is high time that the public recognized its responsibilities in the safeguarding of predatory species just as much as any other integral part of the out-of-doors or any other natural resource. The writings of McAtee (55, 57, 59) and Leopold (47, 50, 52) bring this out with particular force. Without attempting discussion of the little known but complex role of predators in nature, we may say that it ill behooves us to destroy any portion of our heritage, of which we have such scant knowledge. Research findings hint more and more that most native predatory species which have been the object of study could be made to fit very advantageously into a sound system of land use. Whether popular indifference and prejudice will ever permit such biotic possibilities to be fully or even partially realized is problematical.

On the whole, the soundest way to protect a given species—wild or domesticated—from predators is by making it difficult for the predators to prey upon it. In the case of wintering bob-whites, reduction of pressure from one enemy apparently is followed by a compensatory increase of pressure from others as long as the birds are vulnerable from any cause; how much this may be true for summer adults and for eggs and young we do not know.

Stoddard’s work on bob-white nesting indicates that control of nest-destroying enemies may be followed by higher fall population levels. Errington’s nesting and population recovery studies in Wisconsin (23, 26) seem to suggest that ordinary nest destruction may not have such a pronounced effect in determining populations.12

We suspect, nevertheless, that control of nesting enemies may be attended by greater increase of young during the breeding season in northern states. This would mean a larger fall surplus of birds available for sporting purposes. Any increase

12. Wholesale nesting losses, as from drouth [Errington (29)] or from ants [Stoddard (70), (71)], doubtless belong in a different category of significance.
thus to be gained would probably be lost in considerable part, though, unless the shooting were done comparatively early in the season, before any top-heavy surpluses had been exposed too long in environment of shrinking carrying capacity.

**MANAGEMENT OF SHOOTING**

The commonly observed failure of bob-whites to increase under protection beyond a certain level is plainly due in most observed cases to the inability of the environment to accommodate any more than that level. The comparatively rapid recovery of quail populations often to be observed after heavy losses from shooting, starvation, or natural cataclysms seems likewise correlated with the carrying capacity of the environment.

Sportsmen, noting these two population phenomena in a general way, have advanced their hypothesis of inbreeding. By this they have assumed that if quail coveys are not scattered as by shooting, mating will occur within family groups and to the detriment of the species. According to this hypothesis, unshot, inbred populations all but stop breeding and so remain nearly stationary until scattering from shooting breaks up unnatural alliances; with normal mating restored, a healthful acceleration of breeding builds populations up again.

This hypothesis lends itself conveniently as a talking point for those opposed to totally closed seasons on bob-white, and as such it has been avidly propagandized. Others have simply misinterpreted the more or less fragmentary evidence which has come to their eyes, sometimes in a perfectly logical way, or have not recognized the fatal criticisms to which the hypothesis is subject (for discussions, see Stoddard (70, pp. 494-497); Leopold (46, pp. 54-55).)

It is doubtless mainly true that the rate of increase per breeding pair of bob-whites surviving an intensive shooting season is higher than for unshot populations (assuming that the birds have recovered from any shot wounds, etc.); but the same thing seems equally true for the survivors of a drastic starvation emergency. It does not follow that quail need to be shot or starved to breed properly. Shooting, starvation, or anything else of temporary emergency nature that kills large num-

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13. The principal sources of biological evidence against harmful inbreeding of bob-whites in the wild may be briefly listed: (1) Existence of the species in practically unchanged form since at least Pleistocene time; (2) The evident correlation of weight averages with geographic distribution, irrespective of shot or unshot localities; (3) The continual splitting up and recombination of coveys which occurs incidental to rising population densities, and the movements of individuals for considerable distances in response to seasonal and other natural stimuli; (4) The lack of evidence that inbreeding per se would be detrimental to stock of sound genetic composition, even under conditions which may be considerably more favorable to inbreeding than we can conceive of in nature on any important scale.
bers of birds simply serves to lessen population pressure and so accelerates recovery of the surviving population, always provided that reduction of numbers has not proceeded too far. Nor does it follow that the accelerated rate of increase will be enough to compensate in one breeding season for heavy losses suffered before.

It is plain enough that bob-white populations do not increase at rates approaching their breeding potential nor do they increase at rates at all uniform. One may get out paper and pencil and start figuring that so many pairs will average so many young per pair which will give a population of so many birds by fall, but the resulting figures are likely to be extremely misleading.

There is some evidence that we may ultimately be able to calculate bob-white population recovery with fair accuracy, if we know certain essential facts. To do this, we need accurate year to year population records on specific areas and evidence as to carrying capacity of the same areas. We need also some way of evaluating the effects of drouth [Leopold and Ball (53); Errington (29)], disease, cycles [Leopold (48)] and similar obscure but perhaps very powerful influences on reproduction. It is entirely possible that we could well carry on some studies of the potential fertility of the bob-white as Severtzoff (69) has done for certain Old World forms.

Data of good quality on population recovery come in with extreme slowness, but those which we have indicate that the rate of recovery varies inversely with the density of the population in relation to the winter carrying capacity, and possibly the fall carrying capacity, of the environment. In other words, a heavy population in strong environment and a low population in weak environment both show but limited increase after the breeding season; whereas a low population in a strong environment stands a better chance of showing decided increase from seed stock.

At one extreme, we may find well situated remnants of substantial populations recovering from cataclysms at a rate of five or six or perhaps more young per pair. At the other extreme, the increase may amount to less than one bird per pair for populations near environmental carrying capacity [Errington (26)].

Of all the areas which we have studied, the one at Prairie du Sac, Wis., has contributed the most reliable data on rate of increase of populations during the breeding season. These data are singularly reliable because of the large size of the area (5 square miles, or enough to reduce materially the likelihood of much influx or egress during the summer months) and because of the excellent quality of the data secured over a period of years.
The data from this area lend themselves well to tabulation (table 75) and may profitably be studied with care. Since the CWA debrushing for 1933-34 came after the fall census figures were quite complete and since the effects of the debrushing on the cover were largely lost during the 1934 growing season, it is probable that the summer and fall environment as a whole has remained much the same for the period of observation.

**TABLE 75. POPULATION RECOVERY ON 5 SQUARE MILES, EAST OF PRAIRIE DU SAC, WISCONSIN, 1929-34.**

<table>
<thead>
<tr>
<th>Year</th>
<th>April population Birds</th>
<th>(Bird : acres)</th>
<th>December population Birds</th>
<th>(Bird : acres)</th>
<th>Rate of recovery from seed stock during breeding season</th>
</tr>
</thead>
<tbody>
<tr>
<td>1929</td>
<td>227*</td>
<td>1:29.2 A.</td>
<td>121</td>
<td>1:16.4 A.</td>
<td>38%</td>
</tr>
<tr>
<td>1930</td>
<td>112</td>
<td>1:28.5 A.</td>
<td>257</td>
<td>1:12.5 A.</td>
<td>129%</td>
</tr>
<tr>
<td>1931</td>
<td>236</td>
<td>1:13.6 A.</td>
<td>400</td>
<td>1:8 A.</td>
<td>60%</td>
</tr>
<tr>
<td>1932</td>
<td>290</td>
<td>1:11 A.</td>
<td>406</td>
<td>1:7.9 A.</td>
<td>40%</td>
</tr>
<tr>
<td>1933</td>
<td>339</td>
<td>1:9.4 A.</td>
<td>433</td>
<td>1:7.4 A.</td>
<td>25%</td>
</tr>
<tr>
<td>1934</td>
<td>288</td>
<td>1:11.1 A.</td>
<td>411</td>
<td>1:7.8 A.</td>
<td>43%</td>
</tr>
<tr>
<td>1935</td>
<td>196</td>
<td>1:16.3 A.</td>
<td>416***</td>
<td>1:7.7 A.</td>
<td>112%</td>
</tr>
</tbody>
</table>

* During the winter of 1928-29, Gastrow (letter, July 12, 1935) observed the shrinkage of a covey of 30 to about 6, from late December to spring. This was the only covey regularly noted and apparently represented the combined populations of territories No. 5 and No. 13. Since the population of these territories has averaged 8% of the area population, pro-rata calculations would place the number surviving on the area in the vicinity of 22 birds. We think that this number is not far from the number that actually survived.

** The initial figures for the fall of 1935 represent the average for November rather than December and hence may be somewhat high in comparison with the counts for previous years. The population suffered a very slight reduction from shooting in October, however, which may tend to offset any error in this direction.

These data are of particular interest and of application to management, in that they give some inkling as to what may be the effect of over-shooting, and as to what population levels may be most advantageously maintained for sporting purposes.

Unless over-shooting is truly drastic, even if continued it probably never would lead to the progressive extermination of the bob-white in environment at all favorable to the species. The chief effect of moderate though continued over-shooting would probably be to hold populations at some comparatively unsatisfactory level distinctly below the full carrying capacity of the land. We suspect that many quail populations in states having general open seasons are in actuality over-shot and hence may be looked upon more or less as under-populations most of the time—not necessarily insecure under-populations, however.

For that matter, peak populations need not without exception be the ultimate goal of management for sport. Populations of a bird per acre may not be practicable to manage even in strong environment nor even a bird per 2 acres. It may be that a bird per 4 acres may be the optimum level from all standpoints, though the environment may be capable of accommodating twice that population.
Let us speculate that a fall population goal of 433 birds was arbitrarily set for the Prairie du Sac area before any shooting would be permitted. If the continuance of this initial fall level were to be insured, the population probably could not be reduced much below the 339 seed stock level from which the increase up to 433 birds was known to have come. This would permit a take of but 94 birds or 22 percent of the population, including dead birds unrecovered and those lost from crippling. The loss of birds incidental to shooting sometimes amounts to 50 percent of those hit [Errington and Bennett (33); Errington and Hamerstrom (35)], but such a high percentage of loss is commonly avoidable through the use of retrieving dogs and the exercise of more care.

On the other hand, if shooting might begin on a fall population of 257 birds, the stand could be cut down to 112 birds or thereabouts, and still leave sufficient seed stock reasonably to insure recovery up to about the same level by the next autumn. The human toll could then be in the vicinity of 145 birds or 56 percent of the fall population annually, contrasted with but 94 birds or 22 percent at the higher level.

Our data on population recovery are admittedly scant, and any conclusions drawn from them should be distinctly tentative. We do not know if population recovery may ever be worked out by means of formula, even in years when the season’s hatch may be neither extraordinarily good nor bad. We need vastly more accurate data for specific areas over long periods of time.

Studies on experimentally shot game management areas in southern Iowa during the fall and winter of 1933-34 indicate that it is biologically sound to take by shooting that portion of the population which represents the surplus from breeding or that portion in excess of the winter carrying capacity of the land [Errington and Hamerstrom (35)]. In 1933, as measured, this surplus for the Iowa areas under observation seemed to average about 30 percent at the beginning of the winter, judging from the losses suffered by the unshot areas used as checks. This estimate could doubtless be placed higher—perhaps at 40 percent—for late fall populations.

The effect of shooting on over-populations may be somewhat more severe than predation, even though only the equivalent of the vulnerable surplus may be shot. Nevertheless, it is certainly safe to shoot the surplus, whatever that may be for a given area. How much more than the vulnerable surplus may safely be shot we can only guess, in the absence of experimental data on what toll different population levels may actually stand in environments of different carrying capacities.

The administrative difficulties of management of shooting
are tremendous, and on this subject we have very little to contribute. We doubt if quail shooting can be regulated with any great precision. Perhaps the most one can hope for is to keep the shooting, when it is done, under reasonable control. For practical purposes that may be all that is needed, especially if a system could be evolved which would function more or less automatically.

When quail need increased protection—as after cataclysmic emergencies such as drouths, killing winters, etc.—it is to the hunter's ultimate interest to see that they get it, whether that means suspension of his sport for a year or two or not. Total closure of the shooting season may at times have its place in bob-white management, but there are limits as to what should be expected of it. Total closure should be regarded as an emergency measure, but it constitutes no substitute for the fundamental environmental requirements of the species. All the legal restrictions which can be laid down cannot bring about heavy populations of birds on lands having carrying capacities ranging from a bird per 20 to a bird per 40 acres.

A bird per 40 acres population may have a biological surplus, in the sense that we use the term, namely, to denote that portion of the population which is in excess of the carrying capacity of the land and which is doomed to be lost anyway. Nevertheless, the surplus of such a population or even the entire population itself would hardly make a satisfactory shooting, and it would probably be best not to consider shootable any populations under a bird per 10 acres, and preferably not under a bird per 6 acres.

Shooting seasons should come soon after the fall shrinkage of cover, for at this time top-heavy surpluses may be utilized for sport instead of being left to their natural fate. Of course, if the object of management is not to provide shooting, shooting doesn't have to be done. Shooting is not a biological necessity; neither is it a practice necessarily detrimental to the species, if wisely regulated.

Whether shooting is to endure as a sport depends to no small extent upon its followers. Whether it endures may be contingent upon the progress which its followers are able to make in the elimination of the social and biological abuses which have hitherto attended it. These abuses have received much editorial space and are familiar to practically everyone conversant with the subject of hunting. We shall not delineate them here.

POPULATION ESTIMATES

The measurement of existing quail populations is of great practical value in the management of the species. This is true whether an inventory of the wild stock is desired as a basis of
recommendations for a shooting season, or whether the purpose of the measurement may be to evaluate management progress or the havoc of a natural emergency.

Whenever possible, census methods of proved reliability, such as those discussed earlier in this bulletin, should be used in all studies demanding accurate counts. Census-taking, however, is laborious and slow at best. It is not adapted to hasty surveys of large areas, though it should be used locally to check the reliability of approximations derived from less exact but often more practical techniques.

Kendeigh (43) has used the annual Bird Lore Christmas censuses as a basis for calculations of wintering bob-white populations on a state-wide scale. Figures so derived seem to present a remarkably clear picture of the yearly fluctuations in abundance of the bob-white as well as of other species, though they depict general rather than local situations. The Bird Lore census is conducted each year in somewhat the same localities by somewhat the same group of observers. It is sponsored by, and information and data may be obtained from, the National Association of Audubon Societies.

In the course of the quail studies which we conducted on a rather extensive scale in southern Iowa in the fall and winter of 1933-34, we worked out a fairly satisfactory technique of determining approximate populations by marking on a map the territories which "sign" (droppings, dustbaths, feathers, tracks, etc.) showed to be occupied. The effectiveness of the technique is largely dependent upon the skill of the observer in "reading sign" and in recognizing the probable dimensions of the individual covey ranges.

Another technique which served well in very hurried surveys was the estimation of probable covey territories from the road, checked by careful examination of representative environment now and then, just to make sure that the estimated territories were generally being occupied. In this sort of work, a good dog may be used very advantageously, especially when there is no snow on the ground.

On three areas where the pressure of time during the fall of 1933 did not allow even calculations of territory on the basis of sign, Errington made some experimental estimates from the road only, later checking them by actual census work. Of 17 covey territories estimated without actual examination of the land, 16 proved to have been correct [Errington and Hamerstrom (35)]. The checking was entirely independent of the original estimates.

Leopold (48, pp. 378-380) suggests a technique for making habitability tallies of bob-white range from trains or motor cars. These tallies may be made to best advantage if the time of year is that of the critical season and if the range is open
enough to permit identification of food and cover types for at least one ordinary covey cruising radius from each point of observation, or station.

The successful application of the various techniques for estimating quail populations is dependent not only upon the ability of an observer to recognize habitable quail environment when he sees it, but also upon the degree to which the environment is filled to capacity. These techniques are most useful in late fall or early winter checkups, but they have distinct drawbacks as well as advantages.

In the first place, they cannot be substituted for census techniques if census accuracy is required. Commonly, the average size of a bob-white covey is 15 birds, but obviously hard and fast statements as to covey sizes should not be regarded too seriously, since coveys vary all the way from 3 or 4 birds up to 30 or even more. One may flush a given covey as 20 birds one day or as two coveys of 10 each the next. The resulting coveys of 10 may be either widely separated or adjacent, or they may split off from a compact group in flight. Even so, 15 birds is not far from the average number in a fall covey year after year.

If, for any reason, quail populations are decidedly below the carrying capacity of the land over wide areas, the efficacy of estimating techniques is reduced. The 1934 drouth in southern Iowa, for example, precluded the use of any technique which was not at least checked by actual censuses; the birds were simply not present in their usual fall numbers [Errington (29)]. Poaching or unrecorded shooting also may upset population estimates unchecked by field censuses. Populations incompletely recovered from previous winter-killing can hardly be estimated accurately on the basis of the number of birds which ought to be there, though the observer be an experienced judge of territory.

In short, population estimates under conditions favorable to their use may be fairly accurate and quite valuable from the standpoint of administration, but they should always be checked by some careful census work. If the numerical status of bob-white populations is known to be atypical, it may be best not to place any confidence in estimates.

At times, bob-white fall populations may be unusually high, in which event an over-populated condition may often be recognized by conspicuous evidence of predation and mortality from other causes. Granted that the losses are not due to some serious natural emergency, or directly or indirectly to the activities of man, an accelerated fall mortality rate might be welcomed as evidence of a strong population of birds and a substantial surplus.

Reports of hunters and farmers as to numbers of birds have proved almost uniformly to be too inaccurate to be accepted in
lieu of censuses. For purposes of accuracy, the opinion of a farmer who has lived on a place all his life or of a hunter who has covered it for years may frequently be less reliable than a quick size-up of the food, cover and territory relations by one skilled in such work.

Adeptness in evaluating quail range is not anything that requires an academic degree or any formal training, though it does require the scientific attitude of striving to find out only what is true, regardless of what that may be. An observer should be sufficiently familiar with the species so that he will not jump at the conclusion that, because he flushed a covey of quail on the west side of the corn field one day and the same or a different number on the east side of the field the next day, the two coveys must be two different ones. An observer should also be able to count about 20 birds in a covey of 20 instead of guessing that there were 30 or 40.

Almost anyone can learn to census or to estimate quail populations if he has intelligence and the right attitude. The attitude, to our way of thinking, is most important, whatever may be an observer's other qualifications. Unless he can approach a problem objectively, with nothing to prove either way, his statements will always be legitimately subject to discount.

Stoddard (letter, Aug. 27, 1935) suggests a technique we have never tried which sounds very workable. He writes: "I personally use the morning whistling method all through the fall and winter months on doubtful quail territory.... previous to lease or purchase, or where the quail population on a preserve is in doubt, dogs under suspicion, etc. Coveys either whistle from the roost for a few minutes or may be stimulated to do so by a skillful whistler, just at the moment of clear light, especially on fine, quiet and clear mornings. Have frequently roughly located the roosting locations of six to eight coveys from one location on one morning." He considers the method much more reliable in ascertaining the number of coveys than covering the ground once with bird dogs, particularly when the coveys are moving to a limited extent and the conditions for scenting are bad. He suggests for northern studies that "... early morning calling from the roost might be very useful in October and November, before the snows come."

EXPERIMENTATION ON THE LAND

In our bob-white investigations, we have relied primarily upon intensive field observational techniques. We are in agreement with the scientific school which holds that research tends to become more and more a matter of experimentation as progress is made on a specific problem, but it has been our philosophy that for these studies, at least, a substantial foundation of preliminary observational facts needed to be laid first.
A fully balanced program calls for continuous checking of observation by experimentation and vice versa. It also calls for repeated critical analyses and interpretation of existing reliable data, irrespective of conclusions which may have been arrived at, or published along the way.

We feel that, with respect to observational data and critical analyses, our bob-white researches are just beginning to bear tangible fruit. We should judge that our experimental data are much weaker than our observational data, even in elementals, but it cannot be truthfully said that we have no start at all in the experimental stage.

For that matter, our observational data to a considerable extent may correctly be regarded as having experimental values. As a whole, they depict with fair accuracy the response of populations to environmental changes as well as they depict the behavior of birds under comparatively stable conditions. They apply to a vast number of situations, which, if not actually planned in advance by the investigators, often had the virtue of being excellent accidental substitutes for situations of the sort that would have been induced in an experimental program. Indeed, a great many observational data may be as truly experimental in nature as many of those obtained as a result of deliberate manipulation.

Why, for example, should the accurate recording of the effect of environmental changes on a wintering quail population in a given observational area have so much less value if the changes were made by a farmer, undirected and of his own accord, rather than by the investigator himself? Granted that many of the environmental changes—favorable as well as unfavorable to quail—brought about in connection with agricultural practices may not have been planned or even suspected in advance by the investigator, carefully kept records of salient biotic adjustments, combined with data for years previous to and years after the changes had taken place, may nevertheless have substantial utility.

Then, too, we have found that an investigator's control of many of the natural factors affecting wild bob-whites may be so tenuous under even the best of experimental conditions that he cannot rely upon getting experimental data on all phases of life history that he may be studying. Wildlife research often resolves itself largely into getting what apparently significant data can be got, of whatever kinds, wherever, whenever, and however they may come to hand.

The salient advantages of a predominantly observational technique in our quail studies have lain in the comparative ease with which voluminous data under a variety of conditions have been secured. The sheer volume of the observational data on thousands of wintering bob-whites should go a long way
toward compensating for what has not been accomplished by strictly experimental means.

Experimentation on the land, however, is of the utmost necessity in the testing of techniques for bob-white management or the management of any other wildlife species. With regard to this type of experimentation, we are still in a beginning stage, and the ultimate possibilities of trying things out on the land seem to be endless. But to follow a well-rounded experimental program would require funds, time, man power and some control of land beyond that which has so far been available to us.

Mention has already been made of the 1933 experimental shooting program conducted by the Iowa Fish and Game Commission on 14 official game management areas [Schuenke (68)]. One of the objectives of the shooting was to determine experimentally whether the removal of surpluses by shooting in late fall and early winter would lower the vulnerability to predation of the populations wintering on the areas. The experimental shooting related to more than 25,000 acres in 14 areas, of which 10 areas were productive of more or less reliable data. The wintering loss on the 10 shot areas collectively amounted to but 10.3 percent of the population surviving the shooting, contrasted with a collective loss of 28.3 percent on the four similar but unshot areas used as checks [Errington and Hamerstrom (35)].

As a rule, the Iowa program of signing up private farm lands in state game management areas has been of unquestionable effectiveness in the protection of game from poaching. Getting real environmental improvement accomplished by the landholders on these areas, however, has been a tremendous task. With some encouraging exceptions, farm practices on private lands under observation between 1932 and 1935 have continued essentially unchanged as concerns wildlife habitats, agreements to the contrary notwithstanding; hence private lands have not proven to be very productive of data demonstrating what can be expected of practiced management.

We have studied personally five areas which have yielded reliable experimental data on bob-white management. Of these five areas, four represented public land to some degree made available to us for experiments; and the fifth, private land upon which environmental manipulations were conducted at the expense and under the direction of the Iowa Fish and Game Commission. On these areas, changes were actually made in environmental relationships, and the apparent reactions of the quail populations to the changes were noted in greater or less detail. The data resulting from these experiments may be summarized according to areas.

Experimental Area I, including territories number 3, num-
ber 37 and number 44—University Hill Farm, Madison, Wis. (Property of the University of Wisconsin.)

At the beginning of the studies in 1929, the food and cover conditions on this 200-acre sample were both good, but an effort was made to see how high the carrying capacity of the tract could be raised through intensive management. Different types of shelters and feeding stations were also tested.

Grazing was excluded from all brushy lands, and all "cleaned up" practices involving the destruction of brushy cover were discontinued. Clumps of conifers were planted at strategic places, sometimes adjacent to plantings of vigorous thorny rose bushes (Rosa setigera, R. rubiginosa). The conifers (Picea spp., Abies spp., Pinus spp.) were planted as 4 to 6-foot trees, to provide a certain cover value from the beginning. Brush piles of various sizes and types were erected here and there over the place.

Artificial feeding during the first winter was done mainly by means of wheat bundles, used both apart from and in connection with shelters and brush piles.

By the second winter, cover conditions had improved materially on those portions of the area protected from grazing [see Leopold (48, fig. 28 facing p. 316)]. Corn shock feeding stations were freely distributed in desirable places. These improvements apparently resulted in the establishment of a new covey territory in an "odd corner" not previously occupied with any regularity. As the birds ordinarily had easy access to much food in the fields, the corn shocks were used only during severe weather, but at such times they were of indubitably valuable service.

During the third winter, cover conditions were about the same as those of the winter before, but most of the food in the fields was either closely harvested or plowed under. The main reliance of the birds, then, was upon the artificial feeding stations. The feeding program was conducted on a truly substantial scale and seemed to offset with fair adequacy the shortage of food in the fields.

For both the second and third winters, the combined quail and pheasant populations amounted to about one wild gallinaceous bird per 2.6 acres, an evident rise from the average (but fluctuating) stand of about one gallinaceous bird per 6 acres for 1929-30. This rise was attributed to the improvement of food and cover conditions, although we think it highly probable that the same results could have been obtained with far less expense and effort; much of the environment improved was already strong, and the added improvements made no perceptible difference to the security of the resident birds.

During the fourth winter, cover conditions were much as before, but the supply of food in the fields was exceedingly short. No artificial feeding was done, and, as a consequence:
no quail and few pheasants found the area regularly habitable.

**Experimental Area II**, including territories number 9, number 21 and number 22—Fort Des Moines, Iowa. (Property of U. S. Army.)

The sample observational area of about 1 square mile has yielded data of value chiefly in that they have shown the effect of plant succession on the habitability for quail of land withdrawn from cultivation.

Roughly, one-half of the square mile lay in the form of a wooded creek valley, and the other half in uplands which had been planted to cultivated crops prior to 1932. The plant growth on the land formerly cultivated was productive of a considerable amount of quail food (lesser ragweed and smartweed) during the summer of 1932; much less so in the summer of 1933; then, a wholly unexpected growth of lesser ragweed occurred in 1934, possibly as a result of the season's drought.

The nesting conditions on the area and cover relations generally have been uniformly excellent, and strong populations of quail have been observed each fall. The winter environment, however, was deficient from the standpoint of food in 1932-33 and still more so in 1933-34; and the tendency of the populations was to move off the area to adjacent private lands still in cultivation. Food patches were planted and feeding stations were established by the Fish and Game Commission and the Fort Des Moines staff cooperatively, but this artificially supplied food until 1934-35 was apparently incapable of holding more than a few coveys in competition with the winter attractions of cultivated fields outside—especially since many of the outside territories on privately owned farms seemed to be under-populated by reason of fall poaching.

The food situation for the winter of 1934-35 was distinctly improved, aside from the unexpectedly strong ragweed growth. The artificial feeding program was in our judgment adequate to take care of a carrying capacity population for the first time in the 3 years we have had the area under observation. The food patches which held birds were those of fair size (from perhaps a quarter to a half acre), conveniently accessible from good cover.

**Experimental Area III**, including territories number 10, number 23, number 24 and number 60—Des Moines, Iowa, Waterworks Supply Grounds Park and Wildlife Refuge. (Property, city of Des Moines.)

According to Mr. A. F. den Boer, superintendent of grounds, (letter July 12, 1935), there were at least six coveys of quail on the 1,506 acres of the supply grounds before 1930. These, at 15 birds per covey, would amount to 90 birds or one per 16.7 acres. Varying numbers lived on adjacent cultivated private lands.

Cover conditions were excellent on the whole, but the land
had not been cultivated for years, to the natural deterioration of the food types necessary for the wintering of bob-whites. Winter feeding begun in 1928 offset materially the consequent food shortage.

In the summer of 1932, at Mr. den Boer's invitation, the area was inspected and specific recommendations made as to the establishment of feeding stations. These recommendations were followed thoroughly, and a sample area of 300 acres proved very valuable for purposes of study.

The sample 300 acres under heavy feeding wintered a population of at least 55 quail in 1932-33, and nearly 100 in 1933-34.

In order to note the effect of a lapse in feeding operations, we requested that no feeding be done on the sample area in the fall of 1934. The initial fall population was insecurely situated and very restless, and, although feeding in the chief coverts was resumed later in the winter, a population of only 33 birds finished the season on the 300 acres.

The Waterworks data demonstrate, as well as any we have, the importance of an adequate winter feeding program to quail management on primarily uncultivated land. While the quail were fed only in connection with the feeding of bird life generally over the area, and the feeding was done at some expense and purposefully on a scale perhaps a trifle lavish, nevertheless there is a practical lesson here to be gained on one of the things that constitute truly effective management.

**Experimental Area IV,** including territories number 49, number 50 and number 51—Ledges State Park, Boone, Iowa. (Property of Iowa Conservation Board.)

Most of the 500-acre tract under observation is wooded, but some parts are cultivated, thus furnishing an excellent habitat for a limited number of quail coveys. On this tract, through cooperation of Mr. Carl Fritz Henning, custodian, a type of feeding station was devised and tried out—brush pile containing grain—which proved to be extremely effective in giving bob-whites maximum protection from enemies.

**Experimental Area V,** including territories number 67 and number 68—Privately owned farm land, south of Ottumwa, Iowa.

The tract of about 800 acres under observation was set up on private lands as a Bob-white Management Demonstration Area by the Iowa Fish and Game Commission in 1932. This area represented good quail country to begin with, and an attempt was made to improve it further by planting of food patches.

Of the six food patches experimentally planted, only one (see territory number 68) proved to have any apparent influence in raising the carrying capacity of the land. This was located in a cleared space in the woods, at a considerable dis-
tance from regularly habitable winter territories. The addition of the food in this case made habitable a potential territory which previously had not been available. The other food patches simply furnished more food to occupied territories which already had enough for the ordinary needs of their occupants.

All in all, the experimentation upon definite areas has had as its purpose the testing of management measures suggested by the field studies. Food and cover manipulations have received primary emphasis for the reason that they have shown the greatest promise.

Predator control by direct action against predatory species themselves has not been emphasized, as the field studies have indicated very strongly that such would be neither desirable nor efficacious. Aside from a certain amount of hunting and trapping for fur and sporadic hawk and owl shooting by hunters and farmers, predators have not been greatly molested on the majority of the observational areas during the period of study. On but two experimental areas were concerted attempts known to have been made to reduce the resident predator populations, and in neither case could any resulting benefit to quail be recognized [Errington and Hamerstrom (35)].

It is significant that on areas, I, III and IV, the three experimental areas demonstrating the greatest increase or security of quail populations, hawks and owls were not only tolerated but protected, and on area IV a goodly representation of predatory mammals was also to be found. It is so far apparent that quail populations may be about as well maintained at satisfactory levels when predators are many as when they are few, at least within the limits with which our studies have dealt.

Experimentation with the land has not realized its potentialities for bob-white management anywhere. Stoddard has been doing a great deal of work in the Southeast; Leopold et al, in Wisconsin; other investigators, here and there. Bob-white management has been practiced incidental to soil erosion projects, and Holt (41) has reported for the 90,000-acre Coon Valley, Wis., tract an increase of 96 percent in winter population in 1 year's time, despite some adverse circumstances. A few more examples might be listed to illustrate what is being done, but work in this field of endeavor is barely getting started.

As Stoddard (letter, Aug. 27, 1935) writes of the Southeast: "As far as my observations go, this is the only portion of the country where quail management has been practiced long enough, through good seasons and bad, to get much of a line on results." What the ultimate significance of management may be depends largely upon what is done and how well.
Concluding Remarks on Management

Effective northern bob-white management comprises in the main: 1. The raising of the carrying capacity of the land to a satisfactory level or maintaining it there; 2. The strengthening of individual coverts to protect against emergencies such as blizzards and ice storms; and 3. The wise regulation of the human toll upon the species incidental to hunting. Prospective managers should be cautioned that misguided management may lower instead of raise carrying capacity for quail. Particularly is this true on lands that are withdrawn from cultivation and on which the natural plant succession results in the supplanting of quail-food vegetation, as ragweed, by vegetation of lesser value. Deterioration of quail environment may be virtually a certainty in the majority of instances unless the diminishing of the naturally available food supply is offset by artificial feeding or by some continued cultivation.

Experience on game management areas has shown that efforts to raise carrying capacity are more likely to be fruitful if emphasis is placed upon the creation of new covey territories a quarter mile or more distant from territories already occupied. Potential territories strong in either food or cover but deficient in either one or the other may lend themselves exceptionally well to improvement measures.

Satisfactorily located but foodless coverts when supplied with food patches or feeding stations may raise environmental carrying capacity for bob-white, as may open corn or soybean fields when made habitable as territories by the erection of brush piles or the encouragement of dense, shrubby growths along the edges.

Any formula for the management of bob-white which we may try to express at this time could doubtless be refined to advantage as we gain in knowledge. The best management technique we may ever devise will never be infallibly productive of desired results. Quail with or without evident cause may not use territories provided for them. The chance that things may not work out according to hopes is a chance which must be taken by everyone who concerns himself with the management of a wild species, which, after all, does considerably as it pleases.

That continued investigation is the price of greater knowledge should be accepted without question. Wildlife management, to be more than mere tinkering with natural mechanisms, needs not only skilled technicians but manpower capable of difficult ecological research. Persons capable of research can be trained but slowly, for scientifically acceptable research in this field demands abilities equivalent to those demanded by other sciences [Errington (27)].
Administration of wildlife resources is a field in itself and, to be done properly, requires a personnel with background and ability, courage and tact. The ideal administrator must be able to carry on his work with a minimum of entangling politics and at the same time keep reasonably up to date with the progress of significant research. Among other things, he must be able to recognize what constitutes the permanent interests of society and that the duty of a leader is to lead. And in addition, he must be able to guide the mass public, guide them well and make them like it.

The necessity for more harmonious integration of human interests has been touched upon. The first conflicts in human interests doubtless began as soon as there were interests to conflict. Whatever may be the ethical or the biological or the economic aspects of human controversies, the premise is logical that unnecessary friction between groups of people working for a broadly common end imperils the attainment of that end, regardless of how worthy or how desirable of attainment it may be.

We are convinced that there is at least some wholly unnecessary friction between sportsmen and protectionists, in particular. These are two important factions whose one general goal, as repeatedly expressed in their publications, is the conservation of wildlife, non-game species as well as game.

We are aware that shooters exist whose immediate aim is to shoot while they may, irrespective of conservation; and that there are non-shooters who care less for conservation than for the prohibition of shooting. These two extremes may never agree on anything except mutual opposition, but great numbers of sportsmen and protectionists have intermediate viewpoints that should not be quite so irreconcilable.

It seems probable to us that very few sportsmen would deliberately oppose complete legal protection for hunted wild species which they really thought would meet extinction if not given complete protection and which they thought protection would save. Moreover, it seems probable that many of the most militant protectionists would not oppose shooting for sport if they thought that the shooting were being done without actual detriment to the wild populations (especially native species) directly and indirectly affected.

The bob-white is an example of a wild species about which sportsmen and protectionists have long waged bitter controversy, replete with extravagant statements and recrimination. That this controversy should continue with little abatement is especially regrettable in view of the fact that so much of it does not take into account the reliable information to be had.
The provision or maintenance of a suitable environment for the bob-white is of foremost importance, yet of all the things that should never be neglected, this is the one that most frequently is. At the same time, stress—far out of proportion to their value—continues to be laid upon legal protection, predator control, stocking of lands with artificially propagated or imported birds, and other measures that do not remedy fundamental environmental defects.

It has been the observed tendency of sportsmen to magnify the depredations of predators upon game and to minimize the effect of hunting. On the other hand, protectionists have tended to magnify the role of hunting as a decimating factor and to minimize the effect of environmental impoverishment, preventable or unavoidable. The central issues have been further obscured by the perennial argument about inbreeding and by the mutual intolerance and skullduggery from which the strife has not been entirely free.

The sportsman's over-emphasis upon predator control and the protectionist's fear that the bob-white is in continual danger of extermination from over-shooting have been never-failing sources of friction between the two groups. It is hoped that the evidence presented in this bulletin may be a means toward better understanding.

Much of the friction has been due to the failure of the sportsman to recognize that predation upon wing-clipped birds crowded into a rearing pen on a game farm is a different thing from predation upon unhandicapped birds living in the wild under conditions favoring easy escape. Much of the sportsman's animus may trace to observed predation upon over-populations or upon populations conspicuously vulnerable from some cause. The truth of the matter is that predators feed largely upon what prey, game or non-game, that they are able to catch and handle with the least trouble, whether that prey be wild or domesticated; as long as life exists, life will exist to prey upon it, in one way or another.

Leopold (54), (47), (50), (52), has ably written upon the bad aesthetics and the bad politics of ruthless intolerance on the subject of predators. McAtee's (55), (57), (59) essays on predators are much to the point. Some degree of control of some predators will probably always be to the public interest, but discretion should be used as to what predators are to be subject to control and when, where, and how much. The prejudices on this subject, however, are so innate and have gained such terrific momentum, and the plight of so many predatory species is so serious, that efforts could well be made to curtail persecution wherever circumstances permit.

Since there is no apparent justification for stringent predator control in the management of the northern bob-white, and
since the species, given favorable environment, is able to withstand considerable shooting as well, it would seem that as concerns this bird a substantial portion of both hunters and protectionists have less cause for dissension than they may think.

This writing does not contend, nor, in any way, imply that all friction between sporting and protectionist groups may in all respects be eliminated. It does submit that some of the contested issues are not worth the turmoil that they have occasioned.

Leopold (52), referring to the sportsman-protectionist deadlock, warns—“that sportsmen and zoophiles have a common enemy of vastly greater importance to both than any real conflict of interest over hawks, ducks, or the legitimate uses of gunpowder. That enemy is public indifference. The basic issue in wildlife conservation is whether machine-made man, who outnumbers us five to one, really cares enough about wild things to steer the industrial juggernaut around our interests. We [the sportsmen] and the zoophiles are like two small boys quarreling in the street over marbles, unmindful of what is coming down the hill. Unless we make common cause, we bid fair to make only a common grease-spot on the broad highway of progress.”

To many of those who may question the worthwhileness of bob-white management, or the broader wildlife management or the still broader conservation of natural resources, we may not be able to give a very convincing answer. But others may see something of an answer in a final quotation from Leopold (48, p. 388):

“... To see merely what a range is or has is to see nothing. To see why it is, how it became, and the direction and velocity of its changes—this is the great drama of the land, to which ‘educated’ people too often turn an unseeing eye and a deaf ear. The stumps in a woodlot, the species age and form of fencerow trees, the plow-furrows in a reverted field, the location and age of an old orchard, the height of the bank of an irrigation ditch, the age of the trees or bushes in a gully, the fire-scars on a sawlog—these and a thousand other roadside objects spell out words of history of the recent past and the trend of the immediate future ... .

“Biological science, if it had no economic import at all, would nevertheless be justified by its enrichment of the human faculty for observation. Jason, Éric, Magellan, Daniel Boone, saw only the cover of the Great Book. Its free translation is the unique privilege of post-Darwinian explorers. To this first generation of game managers, especially, is offered many a virgin page.”
SUMMARY

This bulletin is based upon the data from intensive population studies which have been carried on with the bob-white quail over a period of six winters, largely in Iowa and Wisconsin agricultural communities. Populations of the bob-white and other wild species have been kept under observation on specific areas for consecutive seasons in order to obtain something of an insight into the ecological mechanisms that govern animal numbers.

Direct enumeration census technique proved to be most useful and reliable in the field researches. Emphasis was placed upon determining the number of bob-whites wintering in a given area and in recording and ascertaining the reasons for any changes in population levels through movements or mortality. The evaluation, as much as possible, of the winter role of food, cover, covey territory, behavior and predation in the life history of the bob-white has been considered of primary importance.

Survival data from the 70 specific bob-white wintering territories or groups of territories which have been studied for more than one season indicate that a given tract of environment is capable of accommodating a rather definitely limited population even under optimum weather conditions. The carrying capacity of a tract of land for bob-whites seems generally to remain about the same from one year to the next, although the carrying capacity of each tract of land is by no means the same. Constancy of carrying capacity has been much more apparent on large land units than on small.

Carrying capacity of quail environment doubtless changes gradually over a period of years, despite the fact that on our chief observational areas it has remained practically constant for as long as 6 years. It is true that given quail environment may often withstand a surprising degree of change without having its carrying capacity appreciably affected, but carrying capacity may be either raised or lowered artificially. What actually determines carrying capacity of quail lands we cannot explain in detail, except that it seems linked with the quality and distribution of food and cover and with the intolerance of over-crowding displayed by the birds themselves.

The correlation between severity of predation upon wintering bob-whites and carrying capacity of their environment is especially significant. Losses from simple predation suffered by wintering populations within the carrying capacity of their environment, as measured to date, have been uniformly light, rarely at a rate exceeding 6 percent per 90 days. On the other hand, when areas were over-populated, either the over-populations were soon reduced by the departure of the excess birds, or
were reduced sooner or later before spring by mortality, usually from enemies. With the vulnerably situated surplus populations gone, the survivors were noted to enjoy a relative security from mortality through predation, except when weakened or handicapped as by starvation, wounds, disease, etc.

While over-populations of wintering bob-whites are commonly reduced through the medium of predation to levels more securely accommodated, the kinds and numbers of the predators do not appear to make a great deal of difference in bringing this about. Populations which were insecure for some reason—notably those portions which were forced into unfavorable environment by crowding or by eviction by man or emergencies from stronger habitats—exhibited a distinct vulnerability to predation, whether predators, within limits observed, were few or many, and whether the predators were or were not of the most formidable types.

Similarly, within limits observed, the comparative abundance of "buffer" species, i.e., mice, rabbits and others which regularly bear the brunt of predator attacks did not appear to make perceptible difference in the intensity of predation suffered by wintering bob-whites. This is probably explainable, at least in part, by the fact that quail seem to be preyed upon more incidentally as they happen to be available than they are eaten as a staple food. Indeed, it probably seldom happens that quail ever constitute enough of an item in the diet of a given predator to rank as a principal food, and we have no evidence that any predator is likely to be dependent upon quail for food under any ordinary circumstances. There are many things which as a rule may be captured for prey with far greater ease than quail except when the latter are rendered vulnerable from some cause.

On the whole, our evidence indicates that the pressure of native enemies is unlikely to be sufficiently severe to reduce healthy, well-fed wintering bob-white populations below the carrying capacity of the land. Populations may be reduced below carrying capacity, however, by shooting or trapping, by starvation or other emergencies associated with snow or ice storms, by drouth, and probably by disease and unknown factors. Concentrations of the exotic ring-necked pheasant in coverts of strategic importance for quail may cause the latter to avoid those coverts, and may thus in effect lower the carrying capacity of the land for the quail themselves.

The seasonal recovery rates of bob-white populations through breeding during the summer apparently have some relation to the position of the spring seed stock level with respect to the fall and winter carrying capacity of the land. The limited data at hand point to considerably higher rates of in-
crease for breeding populations which have been drastically reduced previously by emergencies, over-shooting, etc., provided that the surviving birds are well situated in strong environment.

In the conservation on the management of the bob-white, a few simple measures are to be recommended. The habitability of the environment for quail should be improved or maintained, and this demands particular attention to food and cover. The quail should be subjected to no more than moderate shooting and then only where the species is well established. Intensive campaigning against native predators is not advised, save perhaps under exceptional circumstances where such might be locally desirable; predator control is no substitute for food and cover, and practically all control efforts that we have witnessed in the North have been futile from the standpoint of bob-white management, if not actually detrimental.

All in all, a sound conservation program for the bob-white could well be integrated with a sound program of land use. The bob-white thrives best as a farm species, and the agricultural practices which tend to evict this bird are to a large extent the same practices which tend to evict man himself from the soil. Truly effective bob-white management may be closely correlated in many communities, for example, with the control of soil erosion, of basic significance to permanent agriculture.
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