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6 Population Ecology and Dynamics

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Population Ecology and Dynamics

*L*IKE other animals, grouse and quail exist as natural populations dependent upon particular habitats and vary in population density between the absolute minimum populations that have permitted past survival to fairly dense populations that may approach or even temporarily exceed the *carrying capacity* of the habitat. Each species may also have an upper limit on the density of the population, or a *saturation point*, which is independent of the carrying capacity of the habitat but is determined by social adaptations. Within the population as a whole, individual birds or coveys may have *home ranges*, geographical areas to which their movements are limited and within which they spend their entire lives. Part of the home range may be defended by individuals so that conspecifics of the same sex are excluded for part or all of the year; such areas of localized social dominance and conspecific exclusion are called *territories*. Among species lacking discrete territories and in which the social unit is the covey or flock rather than the pair or family, dominance hierarchies, or *peck orders*, may serve to integrate activities in the flock. These behavioral adaptations and habitat relationships play important roles in population ecology, and will be considered in detail in the individual species accounts. However, a preliminary survey may help to provide generalizations that will be useful to keep in mind when considering individual species.

Natural populations, whatever their densities, have definable structures

in terms of the individuals that make up the population unit. Thus, their sex composition, as defined by *sex ratios*, and age composition, as similarly defined by *age ratios*, provide important information on the proportion of the total population that are potential breeders. The fall age ratio, readily determined by the number of immature birds appearing in hunters' kills, also provides the best information available to the field biologist about the success of the immediately past breeding season.

A final important characteristic of natural populations is the rate at which population recycling occurs, which in turn depends upon the *mortality* and *survival* rates characteristic of it. Mortality and survival are opposite sides of the same coin; as mortality rates increase, average survival probabilities decrease and *life expectancy* (or mean longevity) consequently decreases. Mortality rates can thus be used to determine a statistical measure of life expectancy among individuals of a population, and these data are of basic significance to the field biologist. Regardless of the actual mortality rate, all animals in a population must eventually die; the length of time required for a virtual 100 percent turnover of a population age-class is called the *turnover rate*. This figure corresponds to the maximum possible longevity that may be attained by 1 percent or less of the individuals in that population.

POPULATION DENSITIES

Since virtually all the species of concern here are game birds, information on estimated population densities may be found scattered widely through the technical literature. However, these figures are often not completely comparable; different techniques of census may give different results for the same species, to say nothing of their effects on different species, and the same population may have year-to-year fluctuations that must be taken into account. In addition, census data for some species (such as strongly territorial or lek-forming grouse) are most readily obtained during spring, while fall or winter data may be more readily obtained for species that form coveys and are most conspicuous at that time. Further, some census figures are calculated on the basis of territorial males per unit area, while others consider both sexes. Since the sex ratios of adult populations often differ considerably from a 50:50 ratio, it may be impossible to make the data exactly comparable.

Surprisingly little information is available on minimum tolerable population sizes in the grouse and quail, as Hickey pointed out (1955). These may vary considerably among various species; solitary species such as ruffed

grouse and spruce grouse can perhaps tolerate quite low population densities, whereas highly social species such as quail and socially displaying grouse may have definite minimum thresholds of survival imposed by the physiological stress or inadequate behavioral stimulation of sparse populations. In general, however, the reproductive potential of most grouse and quail species is so great that populations which are drastically reduced by some means have the biological potential for rapid recovery as long as the habitat conditions are favorable. Rather marked population fluctuations are in fact quite common among certain grouse, particularly the arctic populations of ptarmigans and the more temperate populations of ruffed grouse, sharp-tailed grouse, and greater prairie chicken. Estimates of average population density for these species, at least in areas where major fluctuations are prevalent, must necessarily take these variations into account. The existence and possible causes of these periodic population fluctuations are much too complex and controversial to be considered here, and several review papers (such as Hickey, 1955) have dealt with the problem.

It seems evident that, whereas populations may exist over a wide range of densities at the lower limits, upper population densities of a species may have a definite limit. To some degree this is ultimately a habitat-imposed limit, the limiting factors being available food, nesting sites, winter cover, predation, and other density-dependent variables. In addition, territorial size may establish a maximum density, where the habitat might otherwise be capable of supporting a larger number of birds. Even in the absence of actual territorial boundaries the level of intraspecific fighting among reproductively active individuals may force mutual avoidance, causing a maximum spreading out of the population over the available habitat. To the extent that maximum population densities are the result of such species-typical behavioral traits rather than habitat variations, they should be fairly constant for a species in different parts of the species' range. If, on the other hand, maximum densities are primarily a reflection of the differential carrying capacities of the various habitats occupied by a species, they are likely to vary considerably between areas and in the same area from year to year.

In spite of difficulties, for the reasons mentioned earlier, in finding comparable data, it is of interest to compare estimated population densities of the species concerned here. These are in general late winter, spring, or adult breeding population figures (table 15).

Not unexpectedly, quail population densities are in general considerably greater than those of grouse, perhaps reflecting both their smaller sizes and thus lowered food requirements and the far greater sociality typical of these birds. It is generally true that quail densities average at least four times

TABLE 15
SOME REPORTED POPULATION DENSITIES IN FAVORABLE HABITATS
(EXPRESSED IN ACRES PER BIRD)

Sage grouse:	51 acres per male on strutting grounds in spring, Wyoming 13-21 acres per bird during fall in best habitats, Colorado	Patterson, 1952 Rogers, 1964
Blue grouse:	9 acres per adult male, summer average, British Columbia 2.3-7.7 acres per male on summer range, British Columbia 2.5 acres per female; 1.3 acres per male, British Columbia	Fowle, 1960 Bendell & Elliott, 1967 Bendell, 1955a
Spruce grouse:	128 acres per territorial male, Montana 64-90 acres per male (30% of males territorial), Alaska	Stoneberg, 1967 Ellison, 1968b
Willow ptarmigan (red grouse):	3.2-12.3 acres per male in spring, Alaska 4.5-9.0 acres per pair in spring, Scotland	Weeden, 1965b Jenkins, Watson, & Miller, 1963
Rock ptarmigan:	56-109 acres per male, spring, Alaska 4.9-24.7 acres per territorial pair (peak year), Scotland 19.8-74 acres per territorial pair (low year), Scotland	Weeden, 1965b Watson, 1965 Watson, 1965
White-tailed ptarmigan:	12.8-42 acres per adult in summer, Montana	Choate, 1963
Ruffed grouse:	8-38 acres per adult during breeding season, New York 13.5-30 acres per adult in spring, New York 3.4 acres per adult in spring (based on nests), Michigan	Edminster, 1954 Bump et al., 1947 Palmer, 1954
Sharp-tailed grouse:	45 acres per bird in spring, Michigan 16-25.6 acres per bird in late summer, Saskatchewan	Ammann (in Edminster, 1954) Symington & Harper, 1957
Greater prairie chicken:	10-42.7 acres per bird (summary of 4 studies)	Trippensee, 1948
Lesser prairie chicken:	17-38 acres per adult male in spring, Oklahoma	Davison, 1940
Mountain quail:	2 acres per bird maximum spring density, California	Edminster, 1954
Barred & elegant quails:	Under 1 acre per bird locally, Mexico	Leopold, 1959
Scaled quail:	10.1 acres per bird in winter, Texas 0.84 acres per bird in winter, Oklahoma	Wallmo, 1956b Schemnitz, 1961

TABLE 15—(continued)

California quail:	1.7-3.9 acres per bird in late winter, California	Glading, 1941
	0.91 acres per bird in winter, California	Emlen, 1939
Gambel quail:	1.6 acres per bird in late winter, Nevada	Gullion, 1962
Bobwhite:	4-20 acres per bird in spring, good range (various states)	Edminster, 1954
Singing quail:	31 acres per pair, Tamaulipas, Mexico	Warner & Harrell, 1957
Harlequin quail:	21-23 acres per bird in summer, Chihuahua, Mexico	Leopold & McCabe, 1957
	27 acres per pair or family unit, Arizona	Brown, 1969b
Gray partridge:	3.5-5.3 acres per bird in winter, North Dakota	Hammond, 1941
	14-29.4 acres per bird in spring, Washington	Yocom, 1943

greater than do those of grouse, and certainly they show a greater degree of "clumping," because of reduced territorial tendencies and covey-forming behavior. Only the lek-forming grouse species exhibit a corresponding tendency toward contagious distribution patterns, which are related to the males' fidelity to vicinities of their display grounds even when these are not actively being defended. Quail populations also do not regularly exhibit the major oscillations of population density characteristic of some grouse, in spite of the fact that their reproductive potential is extremely high and rapid population increases are thus possible.

FLOCKING AND COVEY BEHAVIOR

Among the grouse, perhaps the best-known examples of flocking and covey formation are to be found among sharp-tailed grouse and pinnated grouse during late fall and winter. These migratory movements, often involving large flocks, were once conspicuous in such midwestern states as Minnesota, Iowa, and Missouri (Bent, 1932). Hamerstrom and Hamerstrom (1951) describe late fall "packs" of sharp-tailed and pinnated grouse that often numbered in the hundreds, sometimes as many as four hundred birds. Similar fall packs of spruce grouse once occurred, and migratory flocks of willow ptarmigan numbering in the thousands have been noted (Bent, 1932). Likewise, rock ptarmigan congregate in relatively large flocks during their seasonal movements to and from their breeding grounds.

In contrast, quail are to be found in coveys at all times other than during the breeding season, and even then nonbreeders may gather in coveys. No doubt for quail the covey represents the most efficient social unit for survival of these relatively defenseless birds, and its formation is facilitated by the reduced territorial tendencies and monogamous pair-bonding behavior of quail. Covey roosting may also be an important means of heat retention during winter. In bobwhites, for example, winter coveys usually consist of about ten to fifteen birds, the most efficient number for retaining heat in circular roosting. The maximum covey sizes of some species is probably a simple reflection of the over-all population density as well as the time of year, but there is a clear tendency for some quail species to form larger coveys than others. Large coveys are especially frequent in southwestern species such as the California quail and scaled quail, as the accompanying summary shows (table 16).

HOME RANGES AND TERRITORIES

Most quails and grouse are fairly mobile, but relatively few undertake true migrations. Vertical migrations are known to occur in such mountain-dwelling species as mountain quail, white-tailed ptarmigan, and blue grouse, and in the last-named species the winter range is actually at a higher altitude than is the summer range. The arctic-breeding rock and willow ptarmigans perform definite seasonal migrations in some areas (Bent, 1932), and Hamerstrom and Hamerstrom (1949, 1951) have summarized data on seasonal movements of the sharp-tailed grouse and pinnated grouse. The home ranges of these fairly mobile species must be the largest of any of the grouse, but detailed data are still lacking. Hamerstrom and Hamerstrom (1951) reported that band returns indicated sharp-tailed grouse movements of up to twenty-one miles, but most returns were obtained within three miles of the point of banding. A few transplanted sharp-tails were also found to have moved more than twenty miles before being shot. Fewer recoveries were obtained for the pinnated grouse, which is apparently the more mobile of the two species. Two banded greater prairie chickens moved as far as twenty-nine miles, and one moved approximately one hundred miles (Hamerstrom and Hamerstrom, 1949). Robel et al. (1970) used radio tracking to determine that greater prairie chicken ranges varied from under two hundred acres in late summer to more than five hundred acres during fall and spring, with adult males having maximum monthly ranges of more than twelve hundred acres during March.

Home range data for the other species of grouse are equally difficult to

TABLE 16

SOME REPORTED COVEY SIZES OF QUAILS AND PARTRIDGES

Mountain quail:	Average of 21 coveys, 9.1 birds, range 3-20	Miller & Stebbins, 1964
Barred quail:	Average of 18 coveys, 12 birds, range 5 to 20 or 25	Leopold, 1959
Scaled quail:	Average of 325 coveys, 31.2 birds, range 4-150 Average of 56 coveys, 19.3 birds	Schemnitz, 1964 Hoffman, 1965
Elegant quail:	Coveys range from 6 to 20 birds	Leopold, 1959
California quail:	Average of 4 winter coveys, 34.8 birds Coveys usually 25-60 but up to 500-600	Sumner, 1935 Leopold, 1959
Gambel quail:	Average of 40 coveys, 12.5 birds, range 3-40 Coveys usually 20-50 birds, but sometimes hundreds	Gullion, 1962 Leopold, 1959
Bobwhite:	Average of 112 winter coveys, 13.8 birds, up to 28 Average of 2,815 winter coveys, 14.3 birds, range 6-25	Stoddard, 1931 Rosene, 1969
Black-throated bobwhite:	Usually 7-15 birds in covey	Leopold, 1959
Spotted wood quail:	From 5 to 10 birds in covey From 6 to 20 birds in covey	Leopold, 1959 Alvarez del Toro (cited in Leopold, 1959)
Harlequin quail:	Average of 62 fall and winter coveys, 7.6 birds, range 3-14	Leopold & McCabe, 1957
Chukar partridge:	From 10 to 40 or more birds in covey	Leopold, 1959

obtain, partly because of difficulties in distinguishing home ranges (occupied but not defended areas) from areas of territorial defense in these species. Males of the forest-dwelling grouse may occupy a fairly large home range and establish territorial limits only where they encounter other males, so that possibly no firm distinction between home ranges and territories may be made (MacDonald, 1968). In the spruce grouse, males may occupy home ranges of 10 to 15 acres, or occasionally as little as three acres (Stoneberg, 1967), but both Stoneberg and MacDonald (1968) found that males spend most of their time within a small portion of their home range. Ellison (1968b) reported that territorial adult males remained on areas of 5 to 9 acres in early May, where display occurred and within which territorial behavior

was seen. All adult males but only some yearlings held territories, and the latter's territories ranged in size up to 21 acres. Other nonterritorial immatures occupied "activity centers" of 6 to 16 acres in size, but sometimes moved more than a mile away from these centers. Nondisplaying or nonterritorial immature males have also been noted in ruffed grouse, blue grouse, and sage grouse. In late May and June the territorial males developed larger home ranges of up to 61 acres, and the nonterritorial birds wandered over areas of from 270 to 556 acres (Ellison, 1968b).

In the ecologically similar blue grouse, territory sizes appear to average somewhat smaller. Boag (1966) and Mussehl (1960) estimated territory size in this species to be from 1 to 2 acres, and Blackford (1963) provides diagrams indicating that eight territories averaged about 5 acres in size. Bendell and Elliott (1967) reported that territories were about 1.5 acres when blue grouse populations were high and from 5 to 11 acres when populations were low. About 30 percent of the males on the breeding range consisted of nonterritorial and wandering immature males. With regard to the forest-dwelling ruffed grouse, Marshall (1965) stated that one male remained within a 10-acre area during April and May, while Eng (1959) pointed out that males usually stayed within one hundred feet of their drumming logs during this period.

In the case of the open-country ptarmigans, several studies on breeding distribution patterns have been done. Weeden (1959) estimated that the territories of willow ptarmigan may range from 3.5 to 7 acres, and the data of Jenkins, Watson, and Miller (1963) suggest that breeding densities of red grouse in Scotland may allow territories of approximately this size, since from sixteen to forty males occupied territories on a 138-acres study area over a four-year period. Similarly, Watson (1965) reported that populations of rock ptarmigan in favored habitats might have territories of 1.2 to 3.5 hectares (3 to 8.1 acres). Schmidt (1969) indicated that the average territory of white-tailed ptarmigan in Colorado is from 16 to 47 acres (with smaller "areas of maximum use"), while Choate (1963) indicated that in Montana this species' territories average about forty by one hundred yards, or slightly less than an acre.

Territories of the lek-forming grouse are the smallest of any of the species concerned here. Dalke et al. (1960) indicated that in the sage grouse the master cocks had a territory forty feet or less in diameter (or 0.03 acre). Lumsden (1965) indicated that the central territories of sharp-tailed grouse were approximately fifteen by twenty-five feet (or 0.01 acre), while peripheral ones were larger. Robel (1965) indicated that territories of male greater prairie chickens varied from 23.6 to 106.5 square meters (or 0.006 to 0.026 acres),

and Copelin (1963) stated that territories of the lesser prairie chicken were only about twelve to fifteen feet in diameter (or 0.002 to 0.004 acres).

Among the quail species, useful application of the principle of territoriality is very limited. Calling or singing by males, at least in the species well studied, denotes the presence of unmated but sexually active males rather than a breeding pair. Thus, in bobwhites, whistling males are simply surplus males (Stoddard, 1931; Bennitt, 1951). The territories of male bobwhites are at most ephemeral and mobile; the female's calls attract sexually active males, whose whistles serve as an advertisement of their presence (Robinson, 1957). The same probably applies to the scaled quail (Schemnitz, 1964). Similarly, in the California quail unmated males establish "crowing territories" near established pairs (Emlen, 1939; Genelly, 1955). Genelly reports that the crowing territories of the excess males may be spaced only about twenty or more feet apart and are as close to established pairs as the latter will allow. Neither California quail nor bobwhites actively defend their nesting sites, and most of the male-to-male fighting involves defense of the mate (Genelly, 1955). In the Gambel quail, pairs gradually form in the winter coveys; the coveys break up as pairs leave and as the unmated males become mutually intolerant and begin to establish individual crowing territories (Raitt and Ohmart, 1966). Estimated winter home range sizes are indicated in table 17 for representative quails. Evidence indicates that the size of these home ranges may vary considerably in different regions and habitats but that they probably average about twenty-five acres in favorable habitats.

The concept of typical territoriality with regard to the gray partridge and the chukar partridge is also of limited application. McCabe and Hawkins (1946) reported that the coveys of gray partridge remain intact until just before nesting. Blank and Ash (1956) report that neither *Perdix* nor *Alectoris* exhibits true territoriality. In the gray partridge establishment of a covey territory is the nearest thing to territorial behavior; covey composition is highly stable in this species. Pairing occurs before the selection of a nesting area, as is also true in New World quails, thus there is no correlation between the selection of mates and the establishment of a nesting area (Blank and Ash, 1956). Mackie and Buechner (1963) agree that typical territoriality is also absent in the chukar partridge. Males repel other males from their mates, thus the female, rather than a geographically defined area, is the object of defense. However, the rally call of mated males may serve to disperse the breeding population in this species (Williams and Stokes, 1965), and population dispersion is thought to be a basic function of avian territoriality.

TABLE 17
REPORTED HOME RANGES OF SOME NEW WORLD QUAILS

Mountain quail:	Nesting pairs occupied from 5 to 50 acres, California	<i>P.R. Quart.*</i>
Scaled quail:	Winter covey home ranges averaged 52.3 acres, Oklahoma	Schemnitz, 1961
	Winter covey home ranges averaged 360 acres, Texas	Wallmo, 1956b
Gambel quail:	Winter covey home ranges averaged 20 acres, Nevada	Gullion, 1956b
California quail:	Winter covey home ranges averaged 26 acres, California	Emlen, 1939
Bobwhite:	Winter covey home ranges averaged 24 acres, Missouri	Murphy & Baskett, 1952
	Winter covey home ranges averaged 24 acres, Texas	Lehmann, 1946
	Winter covey home ranges (1,154 coveys) averaged 13.2 acres and ranged from 4 to 77 acres	Rosene, 1969

**Pittman-Robertson Quarterly* 11 (1951):10.

SEX RATIOS AND AGE RATIOS

The importance of obtaining data about the sex and age composition of game bird populations can scarcely be exaggerated. Such data are generally easy to obtain for the species under consideration here, since reliable techniques for determining sex and age are available for most species. Sex ratio data may provide useful indications of a species' relative reproductive efficiency. For example, adult (or "tertiary") sex ratios in strictly monogamous species such as most quails should clearly be as near 1:1 as possible in order to achieve efficient reproduction, whereas in highly promiscuous or polygamous species a sex ratio strongly favoring females probably represents the most efficient reproductive structure for the population. Nearly all the available data for grouse and quails (except sage grouse and blue grouse) indicate that sex ratios diverge from nearly equal numbers of the sexes at hatching to ratios favoring males in the adult population (table 18). A slight excess of males in renesting species such as

TABLE 18
SOME REPORTED SEX RATIOS
(EXPRESSED AS PERCENTAGE OF MALES IN POPULATION)

	<i>Age Class</i>	<i>Percentage Males</i>	<i>Sample Size</i>	<i>References</i>
Sage grouse	Immatures	45.3	2,693	Patterson, 1952*
	Adults	29.6	1,964	Patterson, 1952*
	Mixed ages	40.0	7,355	Rogers, 1964
Blue grouse	Immatures	50.0	Boag, 1966
	Adults & subadults	40.0	Boag, 1966
Spruce grouse	Immatures	48.3	766	Lumsden & Weeden, 1963*
	Adults	55.3	423	Lumsden & Weeden, 1963*
Willow ptarmigan (red grouse)	Adults	55.9	2,211	Jenkins, Watson, & Miller, 1963*
Rock ptarmigan	Adults	58.5	1,545	Watson, 1965*
Ruffed grouse	Immatures	51.2	17,577	Dorney, 1963*
	Adults	54.6	5,365	Dorney, 1963*
Sharp-tailed grouse	Immatures	56.0	2,108	Ammann, 1957
	Adults	60.0	889	Ammann, 1957
Greater prairie chicken	Immatures	54.9	306	Baker, 1953
	Adults	54.6	298	Baker, 1953
Lesser prairie chicken	Immatures	53.0	491	Lee, 1950
	Adults	47.0	532	Lee, 1950
Scaled quail	Young adults (1st 18 mo.)	47.4	213	Campbell & Lee, 1956
	Old adults (over 18 mo.)	58.9	141	Campbell & Lee, 1956
California quail	Immatures	50.8	6,335	Francis, 1970*
	Adults	57.3	4,347	Francis, 1970*
Gambel quail	Immatures	49.3	333	Raitt & Ohmart, 1968
	Adults	57.8	154	Raitt & Ohmart, 1968
	Young adults (1st 18 mo.)	51.4	215	Campbell & Lee, 1956
	Old adults (over 18 mo.)	55.8	525	Campbell & Lee, 1956
Bobwhite	Immatures	50.5	34,989	Bennitt, 1951
	Adults	59.0	7,521	Bennitt, 1951
Harlequin quail	Mixed (museum sample)	63.0	502	Leopold & McCabe, 1957
Gray partridge	Adults	58.0	115	McCabe & Hawkins, 1946
	Mixed	51.0	14,167	Johnson, 1964*
Chukar partridge	Mixed	50.0	116	Harper, 1958

*Calculated from data presented by authors.

TABLE 19
SOME REPORTED FALL AND WINTER AGE RATIOS
(EXPRESSED AS PERCENTAGE OF IMMATURES IN POPULATION)

	<i>Percentage Immature</i>	<i>Sample Size</i>	<i>References</i>
Sage grouse	57.8%	4,657	Patterson, 1952
	51.4%	7,355	Rogers, 1964
Blue grouse	65% (late summer)	Boag, 1966
	57-65%	Hoffman et al. (cited in Bendell, 1955a)
Spruce grouse	64.4%	1,189	Lumsden & Weeden, 1963*
Willow ptarmigan	72%	5,266	Bergerud, 1970b
Rock ptarmigan	73-77%	Cited in Choate, 1963
White-tailed ptarmigan	33-47%	Choate, 1963
Ruffed grouse	77%	22,942	Dorney, 1963*
Sharp-tailed grouse	70%	3,926	Ammann, 1957
	63.5%	16,283	Johnson, 1964*
Greater prairie chicken	50.2%	604	Baker, 1953
Lesser prairie chicken	53.2%	932	Lee, 1950
Mountain quail	48%	198	Leopold, 1939†
Scaled quail	74%	1,219	Schemnitz, 1961
California quail	63.3%	5,603	Emlen, 1940*
	59.3%	10,682	Francis, 1970*
Gambel quail	76%	352	Raitt & Ohmart, 1968*
Bobwhite	82.3%	51,178	Bennitt, 1951
	82%	1,546	Marsden & Baskett, 1958
Harlequin quail	61%	57	Leopold & McCabe, 1957†
Gray partridge	79.5%	14,167	Johnson, 1964*
Chukar partridge	87-89.5%	Johnson, 1960

*Calculated from author's data.

†Based on museum skin samples taken at various times of year.

most quails may not be undesirable, inasmuch as it may assure that sexually active males will be available to fertilize reneating females whose mates have already reached a postreproductive condition. On the other hand, males of polygamous or promiscuous species may be selectively harvested without significantly reducing the reproductive potential of the population. Among such species in which only a single sex is hunted, pre hunting and post hunting sex ratio changes provide a valuable means of calculating population sizes (Davis, in Mosby, 1963).

The acquisition of age ratio data is at least as important to biologists as a knowledge of sex ratios in wild populations. Hickey (1955) reviewed the history of age ratio studies and their application for wildlife biologists. He also summarized the then available data for age ratios of gallinaceous birds. In table 19 additional age ratio data are summarized, which for the most part have been chosen to supplement rather than to duplicate those figures provided by Hickey.

Age ratio data have two immediate applications. One such application is that they provide a means of estimating survival rates for relatively short-lived species, without the necessity of marking birds individually and obtaining recapture or recovery data. Marsden and Baskett (1958) used the technique of assuming that the percentage of immature birds in the fall hunting sample represented an estimate of the annual mortality rate of adults, and indeed these estimates are generally in close agreement with mortality estimates based on data from banded birds as summarized by Hickey (1955).

The second and more generally applicable use of age ratios is to supplement the evidence obtained from nesting and brood counts about the relative success of the past breeding season. By comparing the number of immature birds in the fall population with that of adults (or adult females, as is done by some investigators), an estimate of breeding productivity is possible. Thus, a ratio of 50 percent immatures to 50 percent adults in the fall kill sample would suggest a breeding season productivity of 100 percent, while a ratio of 75 percent immatures to 25 percent adults would provide a productivity factor of 300 percent. The ultimate limit on such productivity factors is determined by the average clutch size of the species, and the difference between the actual productivity ratio and the potential one (assuming an equal sex ratio in adults) might provide an estimate of the reproductive efficiency of the population. For example, a quail species with an average clutch size of twelve could attain a fall population of 86 percent immatures if conditions were ideal. A figure in excess of this would suggest that double-brooding might have occurred,

or that an error in estimate resulted from differential sampling vulnerability of the two age classes.

Reported age ratio data for as many species of grouse and quail as possible are summarized in table 19. It should be apparent that such data are likely to vary considerably in different years or under different ecological conditions. Nevertheless, such data provide sample figures for interspecies and intraspecies comparisons and for illustrating the theoretical relationship just mentioned between clutch size and potential productivity. When tertiary sex ratio data are available, the possibility of inserting a correction factor based on the percentage of adult females in the breeding population is of course desirable.

MORTALITY AND SURVIVAL RATES

It has been emphasized that populations of animals can vary in density, in spatial distribution patterns (territoriality favors dispersion, sociality favors clumping), and in sex and age composition. Not only can the population be analyzed for immature and adult components but the adults themselves have age composition characteristics, with the relative frequency of the various age classes depending on the rate at which the animals die. It is possible to gather such mortality information only by marking individuals (preferably while still young enough to determine their exact age at the time of marking), releasing them, and resampling the population at later times to determine how long the marked individuals survive. A review by Farner (1955) provides the theoretical concepts and practical methods that are required in the performance of such investigations with birds, and it is beyond the scope of this short review to mention them here. A few ideas, however, are so basic to the understanding of this aspect of population dynamics that they must be considered individually.

The relative rate at which individuals in a population die is usually expressed as an *annual mortality rate* (M), which is the ratio of those individuals dying during a year to the number that were alive at the beginning of the twelve-month period, whatever its starting point. The *annual survival rate* (S) is the opposite ratio: the proportion of the animals still surviving at the end of a twelve-month period to those that were alive at its start. Thus, $S+M=1.0$, or $S=1.0-M$. Some examples of estimated survival rates appear in table 20. The total population may be subdivided into different *age classes* according to the year in which each individual was hatched. The population thus consists of varying numbers of one-year-olds, two-year-olds, etc. For the species under consideration here, all the individuals in a single age class will probably have actual ages

TABLE 20
SOME REPORTED ANNUAL ADULT SURVIVAL RATES

	<i>Survival Rate(s)</i>	<i>Reference</i>
Blue grouse		
Males	73%	Zwickel, 1966
Females	62%	Zwickel, 1966
Adults	72%	Bendell & Elliott, 1967
Yearlings	73%	Bendell & Elliott, 1967
Willow ptarmigan		
Norwegian race	22–23%	Hagen (cited in Hickey, 1955)
Scottish race	29–33%	Jenkins, Watson, & Miller, 1963
Newfoundland race	28%	Bergerud, 1970b
Ruffed grouse		
Adult males	47%	Gullion & Marshall, 1968
Greater prairie chicken		
Both sexes	28–38%	Hamerstrom & Hamerstrom, 1949
Sharp-tailed grouse		
Both sexes	40%	Ammann, 1957
California quail		
Immatures	26.7%	Raitt & Genelly, 1964
Adults	31.6%	Raitt & Genelly, 1964
Gambel quail		
Both sexes	28–40%	Sowls, 1960
Bobwhite		
Both sexes	22%	Marsden & Baskett, 1958
Gray partridge	20%	Westerskov (cited in Hickey, 1955)

within two or three months of one another, depending on the length of the breeding season. Each breeding season thus generates a new *cohort* of birds that have hatched during the same year and constitute a single age class. The length of time required for an entire cohort of hatched young to be essentially eliminated from the population is referred to as the *turn-over period* or *turnover rate*. This is perhaps properly estimated on the basis of time required for 100 percent of the age class to be reduced to 1 percent of the original cohort, but practice varies in this regard (Hickey, 1955). The means proposed by Petrides (1949) for calculating an expected

turnover rate is based on the assumption that the mortality rate is constant for all ages. It is therefore convenient to define the initial cohort as, for example, the birds alive at the start of the first October following hatching to avoid the problems of the higher mortality rates usually associated with the first few months of life. Obviously, turnover periods having a starting point consisting of 100 percent of the immatures surviving to fall will be longer than those based on a cohort of newly hatched young. Even shorter would be turnover rates based on 100 percent of the potential young, in the form of the total eggs laid. Although this last basis for defining a cohort is rarely if ever used in practice, it has one theoretical advantage. That is, by starting with the eggs laid rather than with some later stage, it is possible to introduce differential rates of prehatching, juvenile, and adult mortality rates in the construction of a *survivorship curve*, which not only provides a more realistic view of population diminution, but also introduces the possibility of calculating the rate of egg replacement potential in the adult age classes of the resulting survivorship series. This must be based on average clutch size estimates, knowledge of possible nonbreeding rates in younger age classes, and tertiary sex ratio information, but it provides a useful means of estimating the population regeneration potential of species having varying mortality rates of eggs, juveniles, and adults. Some examples of such calculations are presented in figures 13 to 15.

One of the most useful statistics that can be derived on the basis of known and constant mortality rates is an estimate of further *life expectancy* as of a prescribed initial date or age. Thus, a life expectancy figure may be defined as of the date of hatching, the date of fledging, or some later chosen time. In general, it is perhaps best designated for birds as the earliest age at which juvenile mortality rates have decreased to the point where they become virtually identical with adult mortality rates. This may be as early as the first September or October after hatching or possibly even a year later. In any case, the further life expectancy for any age class is in effect the length of time required to reduce the number of surviving individuals of that age class by 50 percent. The expectation of further life is thus an estimated *mean after lifetime*, or a mean longevity as of a selected initial date. Farner (1955) has suggested that an estimate of a mean after lifetime can conveniently be calculated, by using the following formula, if the mean annual mortality rate is known and if the mortality rate of the included age classes do not differ significantly from the over-all mean mortality rate:

$$\text{Mean after lifetime} = \frac{0.4343}{\text{Log}_{10} S}$$

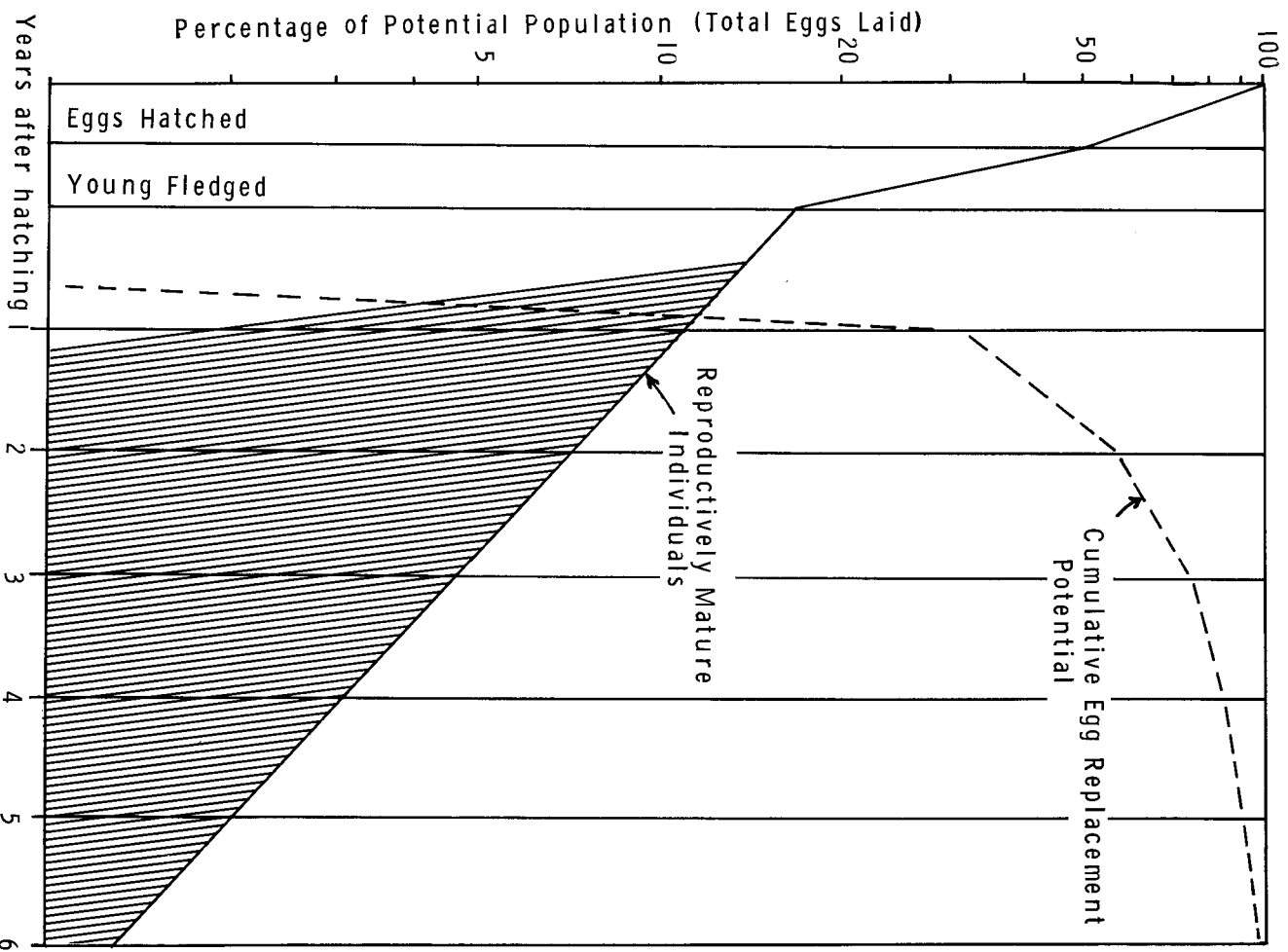


FIGURE 13. Calculated survival curve and egg replacement potential of female blue grouse based on field data. (Assumptions are of a 50% hatching and 33% rearing success, 62% annual survival after first fall, and an average clutch size of 6.2 eggs, with 25% of the first-year females nonbreeders.)

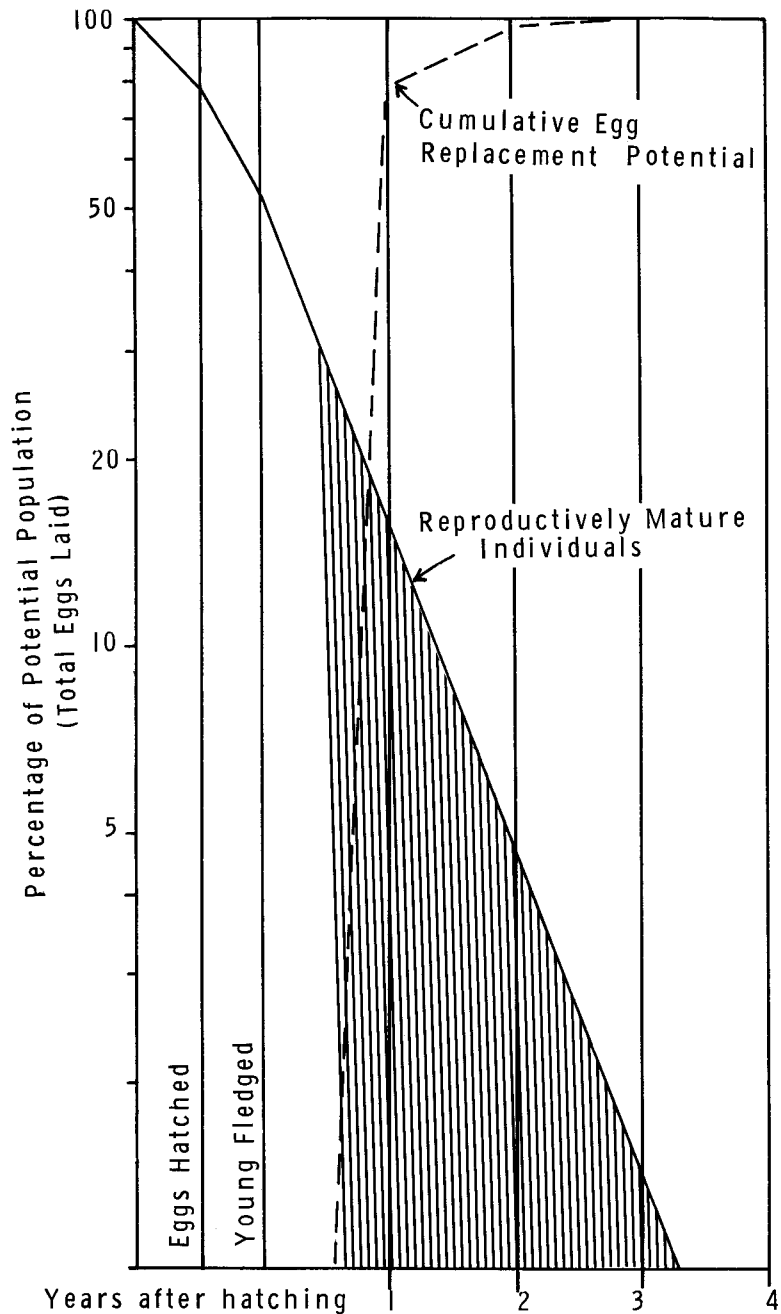


FIGURE 14. Calculated survival curve and egg replacement potential of willow ptarmigan. (Assumptions are of a 77% hatching and 33% rearing success, a 44% annual survival rate of both sexes after first fall, and an average clutch size of 7.1 eggs.)

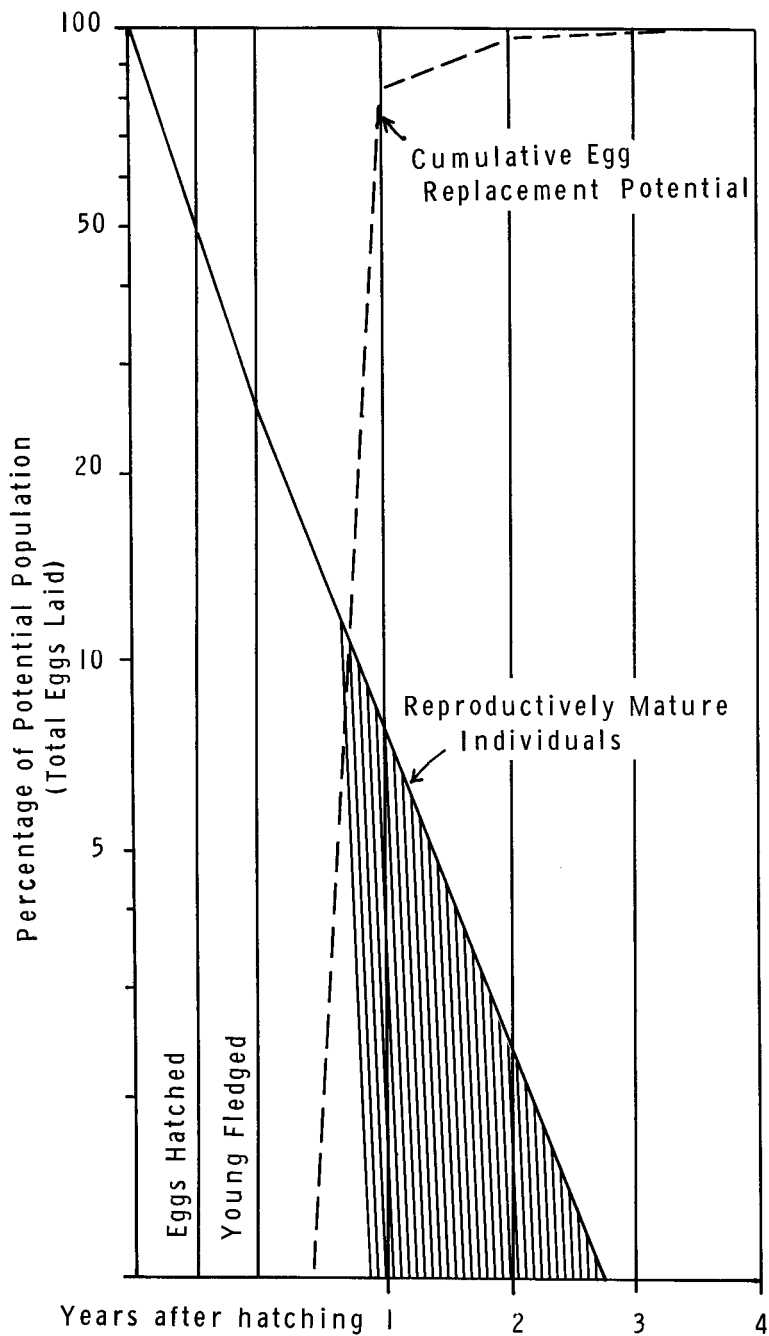


FIGURE 15. Calculated survival curve and egg replacement potential of California quail. (Assumptions are of a 50% hatching and 50% rearing success, a 42% annual survival of both sexes after the first fall, and an average clutch size of 14 eggs.)

If the selected initial date from which a mean after lifetime is calculated is chosen as some point following hatching rather than hatching itself, then of course the estimated mean after lifetime is not the same as the average life span. Rather, the average life span (or mean total longevity) will be somewhat less than the sum of the mean after lifetime estimate and the interval between hatching and the initially selected date, with the difference dependent on the higher mortality rates between hatching and the initially selected date. It might be noted that Lack (1966) has provided a convenient formula for computing further life expectancies in years by the following method, in which M equals the annual mortality rate:

$$\frac{2-M}{2M}$$

Recently, a valuable contribution by Ricklefs (1969) has concentrated on the significance of mortality rates of eggs and young, and he has provided a ready method of estimating short-term (weekly, daily, etc.) mortality rates for these important stages in the life cycle. He found that such mortality rates can be calculated by the equation:

$$m = \frac{-(\text{Log}_e P)}{t}$$

where m equals the mortality rate per unit of time (t) and P equals the proportion of nests or individuals surviving the total period considered, again assuming that mortality rates are constant throughout the entire period. As noted in the previous chapter, daily nest mortality rates are generally between 2 and 4 percent, whereas chick mortality rates are considerably lower (Ricklefs, 1969).

An equally useful formula is that proposed by Petrides (1949) for estimating the turnover period, this term being defined as the time required to reduce an original age-class cohort of 100 percent to its virtual elimination from the population. Such an effective end-point might be 5 percent, 1 percent, or 0.1 percent, depending on one's views. Petrides reported that the turnover period can readily be calculated by the following formula, again assuming that the mortality rate of different age classes does not vary significantly from the over-all annual mortality rate:

$$\text{Turnover period (years)} = \frac{\text{Log}_{10} \text{ of surviving fraction of cohort}}{\text{Log}_{10} S} + 1$$

If 1 percent is chosen as the surviving fraction of the cohort that represents the virtual elimination of an age class from the population, then the formula can be restated simply as:

$$\frac{-2.0}{\text{Log}_{10} S} + 1$$

In table 21 are presented some calculated mean after lifetimes (usually after the first fall of life) and estimated turnover periods among various species for which annual mortality estimates have been reported. In some cases these estimates of mean after lifetimes differ slightly from those reported by the original authors, the variations being the result of different techniques or assumptions, but in general the estimates are very close to those published earlier for these species.

Such calculated turnover periods should provide at least a general estimate of potential natural longevity, as represented by the oldest age class that might be encountered in natural populations. Potential natural longevity is likely to be less than potential longevity under ideal conditions, such as optimum conditions of captivity. In table 22 are presented some reported estimates of mean after lifetimes and records of unusual longevity for wild or captive individuals. It would seem that four or five years represents close to the potential natural longevity of most grouse and quail species, but available mortality rates of a few species (especially blue grouse and white-tailed ptarmigan) indicate that it might be considerably longer than this.

TABLE 21
SOME LONGEVITY ESTIMATES, BASED ON REPORTED SURVIVAL RATES

	<i>Survival Rate(s)</i>	<i>Mean Longevity after 1st Fall*</i>	<i>Maximum Longevity and Turnover Period †</i>	<i>References</i>
Blue grouse				
Males	72.5%	3.1 yr.	15.3 yr.	Zwicker, 1966
Females	62.0%	2.09 yr.	10.6 yr.	
Willow ptarmigan				
Both sexes	30.0%	10 mo.	4.8 yr.	Jenkins, Watson, & Miller, 1963
White-tailed ptarmigan				
1st yr.	37.0%	0.99 yr.	Overall (57.9% S) 9.4 yr.	Choate, 1963
After 1st yr.	71.0%	2.92 yr.	After 1st yr. 14.4 yr.	
Ruffed grouse				
Males (after 1st winter)	47.0%	1.25 yr.	6.76 yr.	Gullion & Marshall, 1968
Sharp-tailed grouse	40.0%	1.10 yr.	6.0 yr.	Ammann, 1957
Greater prairie chicken	28.38%	11 mo.-1.1 yr.	9.4 mo.-1.03 yr.	Hamerstrom & Hamerstrom, 1949
California quail	28.8%	9.6 mo.	4.7 yr.	Raitt & Genelly, 1964
Bobwhite	22.0%	7.9 mo.	4.0 yr.	Marsden & Baskett, 1958
Gray partridge	20.0%	7.4 mo.	3.9 yr.	Westerskov, (cited in Hickey, 1955)

*Method of Farner (1955:409).

†Method of Petrides (1949), using 1% of original cohort as end-point.

TABLE 22

SOME LONGEVITY ESTIMATES AND MAXIMUM LONGEVITY RECORDS

Sage grouse:	One banded female was recovered 7 years after banding. Returns of marked birds returning to strutting grounds one year later varied from 5 to 21 percent over 3 years. Dalke et al., 1963
Willow ptarmigan (red grouse):	Seven birds at least 4 years old were recovered from 12,050 banded. Estimated mean longevity of about 1 year from August following hatching. Jenkins, Watson, & Miller, 1963
White-tailed ptarmigan:	Twelve of 36 females and 16 of 31 males lived at least 5 years. Estimated mean longevity after first summer, 3.02 years; estimated maximum longevity of 13-15 years. Choate, 1963
Ruffed grouse:	Maximum known survival of 94 months by 1 of 978 marked birds. Mean life-span of 8.56 months for immature females; 8.63 months for immature males. Mean life-span of birds banded as adults was 25.3 months for males, 23.7 months for females. Gullion and Marshall, 1968
Sharp-tailed grouse:	One bird at least 7.5 years old from 93 banded birds. Mean longevity after full growth estimated from 1.51 years (females) to 1.61 years (males). Ammann, 1957
Greater prairie chicken:	Two birds, out of 597 banded, recovered in fourth year after banding. Hamerstrom & Hamerstrom, 1949
California quail:	One male banded as an adult was recaptured when at least 80 months old. Mean life expectancy after September following hatching is 9.7 months. Raitt and Genelly, 1964
Gambel quail:	Four out of 121 birds trapped as adults were alive 4 years later, and 10 out of 321 birds trapped as juveniles were alive 4 years later. Sowls, 1960
Bobwhite:	One out of 1,156 banded bobwhites was recovered in its fifth year. Estimated life expectancy after October following hatching is 8.5 months. Marsden and Baskett, 1958. In captivity known to live at least 8 years, still fertile at four to five years of age. Stoddard, 1931. One report of a captive individual surviving 9 years. Judd, 1905a