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$\mathcal{T}HE$ reproductive potential of animal species is a compound result of numerous behavioral and physiological characteristics, most of which can be considered species-typical. These include such things as the time required to attain reproductive maturity, the number of nesting or renesting attempts per year once maturity is attained, the number of eggs laid per breeding attempt, and the number of years adults may remain reproductively active. These traits place an upper limit on the reproductive potential of a species, which is never actually attained. Rather, the actual rate of increase will only approach the reproductive potential, being limited by such things as the incidence of nonbreeding; the mortality rates of adults; decreased hatching success resulting from infertility, predation, or nest abandonment; relative rearing success; incidence of renesting and clutch sizes of renests; and similar factors that affect the reproductive efficiency. The relative involvement of the male in protecting the nest or the young may also influence hatching or rearing success. Among those species in which the male does not participate in nesting behavior, the relative degree of monogamy, polygamy, or promiscuity may strongly influence the reproductive ecology and population genetics of the species. Although many of these considerations will be treated under the accounts of the individual species, a general comparison of the grouse and quail groups as a whole are worth considering here, to see if any general trends can be detected.

AGE OF SEXUAL MATURITY AND INCIDENCE OF NONBREEDING

In the absence of evidence to the contrary, it must be assumed that all native quail species mature their first year. This is indicated by the apparent absence of nonbreeding females during favorable years under natural conditions, known regular breeding by females still carrying juvenal outer primaries, and consistent breeding under captive conditions of birds less than a year old. Bobwhites reared in captivity usually attain sexual maturity at between 139 and 185 days under lighted conditions (Baldini, Roberts, and Kirkpatrick, 1952), and scaled quail have laid fertile eggs in our laboratory within 160 days after hatching. We have also regularly obtained breeding from yearlings of all other quail species we have maintained in captivity.

Among the grouse, the situation may be different for at least some species. Bump et al. (1947) reported that nonbreeding by wild female ruffed grouse varied from none in most years to over 25 percent in some years. Weeden (1965b) found no indications of female nonbreeding in wild rock ptarmigan, although Maher (1959) found some evidence of nonbreeding in wild willow ptarmigan. Stanton (1958) reported that 25 percent of yearling female sage grouse failed to produce eggs, and Bendell and Elliot (1967) found that 25 percent of thirty-eight yearling female blue grouse were nonbreeders, compared with 4 percent of sixty-nine adult females. Yearling male blue grouse are nonterritorial according to these authors. Yet in this species, as in several other grouse, the highly promiscuous mating system allows for the achievement of effective fertilization of all females by a relatively small proportion of fully mature males.

Extensive nonbreeding during unfavorable years is apparently much more prevalent among quails than grouse, at least among the more northerly species of quails. Mountain quail may not nest at all in very dry years (Leopold, 1959). The same applies to scaled quail; precipitation occurring during the current spring and summer seems to be the most important influence on this species (Campbell, 1968). Little or no rainfall during the preceding winter and spring reduces the over-all nesting success of the California quail (Hungerford, 1964). Similarly in the chukar partridge extensive nonbreeding may occur in unusually dry years (Christensen, 1954), and the same may apply to bobwhites (Lehmann, 1946).

NUMBER OF NESTING OR RENESTING ATTEMPTS PER YEAR

No known instances of double-brooding have been reported for any North American grouse, and, indeed, known examples of renesting when nests are

lost after incubation has begun are hard to find. Among the white-tailed ptarmigan Choate (1963) reports one definite renest; and the late clutches number only three or four eggs. Weeden (1965b) reported only one known case of renesting in rock ptarmigan, but noted that 3 percent of 228 nests and broods were late-hatching. Jenkins, Watson, and Miller (1963) mention that among Scottish red grouse definite renesting occurs in some years, and the clutch sizes of second nesting attempts are sometimes smaller than in first ones. They noted that five of seven marked birds laid again after their eggs were taken. Patterson (1949) estimated that a small incidence of renesting probably occurs in sage grouse, and Crunden (1959) subsequently reported one definite case. Stoneberg (1967) found no indication of renesting in the spruce grouse, and so far only two definite cases of renesting in the blue grouse have been reported (Zwickel and Lance, 1965). Renesting by ruffed grouse is apparently infrequent (Bump et al., 1947), with probably less than 25 percent of the unsuccessful females attempting to renest (Edminster, 1947). Ammann (1957) reported that no more than 10 percent of young sharp-tailed grouse hatched in Michigan could have resulted from renesting. Nests of the greater and lesser prairie chickens show a decline in clutch size toward the end of the nesting season (Hamerstrom, 1939; Baker, 1953; Copelin, 1963), suggesting a certain incidence of renesting, but until recently only in the Attwater prairie chicken had any verified cases been reported (Lehmann, 1941). However, Robel et al. (1970) found that three of fourteen radio-tracked greater prairie chicken females renested, one of them making two renesting attempts.

In contrast, the quail as a group show a greater tendency toward double-brooding and renesting, perhaps because of their monogamy and generally more southerly breeding distributions. Leopold (1959) reports that one or two renesting attempts may be made by mountain quail, but very early accounts suggesting that two broods of this species or of scaled quail are sometimes reared are yet to be verified. Evidence favoring double-brooding is strongest for the California and Gambel quails. McMillan (1964) reported that in favorable years up to 75 percent of the early broods of California quail are reared by males while the females renest. McLean (1930) reported one definite second brood in this species. Edminster (1954) states that there may be up to two renesting attempts, and Raitt (1960) stated that a few late broods hatched in August indicate probable renesting behavior. In the Gambel quail renesting attempts are reportedly common until mid-August (Gorsuch, 1934) or even early September (Raitt and Ohmart, 1966), and possible extensive double-brooding during a favorable year has been reported by Gullion (1956a), who believed that the earlier birds may be either cared for by males or left in the care of older birds of the year. Stanford (1953)

reported that three captive pairs of bobwhites raised two broods, with the male taking over the first in each case.

Renesting in the gray partridge is highly probable. McCabe and Hawkins (1946) indicated that the average clutch size of probable renests is 9 eggs, or considerably under the clutch size of early nests. Mackie and Buechner (1963) suggested that in chukar partridges renesting until early July is probable in Washington state; in Turkey renesting occurs if the first nest is broken up early in incubation (Bump, 1951). The role of the male in the chukar partridge is still uncertain; in this species and the related redlegged and Barbary partridges the male evidently sometimes incubates the first nest while the female lays a second clutch (Goodwin, 1953). Watson (1962a) suggests that perhaps the male raises a brood when the population is low. Observations in the United States sometimes suggest that males may play no role in incubation and instead gather in flocks (Alcorn and Richardson, 1951; Bohl, 1957). Other studies indicate that males may be seen with about 10 percent of the females and broods (Mackie and Buechner, 1963) or may accompany broods fairly often (Galbreath and Moreland, 1953).

PARTICIPATION OF THE MALE IN INCUBATION
AND DEFENDING THE BROOD

Since the availability of the male influences the likelihood of successful renesting and allows for possible double-brooding, a summary of male participation in breeding is of some interest. Among the grouse, no cases of male incubation have been reported. However, the male willow ptarmigan actively defends the nest and brood (Dixon, 1927; Conover, 1926; Watson and Jenkins, 1964). In the rock ptarmigan the male rarely stays with the brooding female and does not defend the brood (Weeden, 1965b) or if present may desert the brood when they can fly or even earlier (Bannerman, 1963). However, some instances of active brood defense have been seen by MacDonald (1970). In the white-tailed ptarmigan the male plays no part in the incubation or care of young (Choate, 1960).

Association of the male with the nest and brood is well established for most of the New World quails and introduced partridges. In a few species the male regularly assists in incubation or may occasionally assume the entire incubation duties. This has been reported in bobwhites (Stoddard,

1931), scaled quail (Schemnitz, 1961), and harlequin quail (Willard, in Bent, 1932). Males may also assume incubation duties if the female dies, as has been noted in bobwhites (Stoddard, 1931), Gambel quail (Gorsuch, 1934), and California quail (Emlen, 1939; Price, 1938). Some possible examples of a male's incubating the first nest so that the female may begin another were mentioned earlier for California quail, Gambel quail, and chukar partridge. In the gray partridge the male may possibly assist in incubation (Hart, 1943) and will typically remain with and defend the brood (McCabe and Hawkins, 1946).

Males of most New World quail species, whether or not they have actually assisted in incubation, will normally remain with the brood and defend it. Males are regularly seen attending females and broods of scaled quail (Schemnitz, 1961), mountain quail (Dawson, 1923; Bent, 1932), Gambel quail (Gorsuch, 1934), bobwhites (Stoddard, 1931), and California quail (Genelly, 1955; Emlen, 1939), in the last of which even broodless males may guard the young. Little information on this behavior is available for the tropical forest-dwelling species, but Skutch (1947) indicated that in the marbled wood quail (*Odontophorus gujanensis*) males participate in brood care. This also seems to apply to the harlequin quail (Leopold and McCabe, 1957), and to the singing quail (LeFebvre and LeFebvre, 1958).

CLUTCH SIZES AND EGG-LAYING RATES

The rate at which egg-laying in birds occurs presumably depends on how rapidly follicles can be ovulated and associated albumen can be secreted by the female, and for the species under consideration here this generally averages slightly more than one day per egg. Some estimates for various grouse species are 1.1 days per egg for rock ptarmigan (Westerskov, 1956), 1.3 days per egg for sage grouse (Patterson, 1952), and 1.5 days per egg for ruffed grouse (Edminster, 1947). Corresponding figures for quails and introduced partridges include 1.1 days per egg for bobwhite (Stoddard, 1931), 1.1 days per egg for gray partridge (McCabe and Hawkins, 1946), 1.3 days per egg for chukar partridge (Mackie and Buechner, 1963), and 1.4 days per egg for California quail (Genelley, 1955). Thus, in general, a clutch perhaps takes a few days longer to complete than there are eggs laid.

Clutch size data are difficult to be confident about, for not only do these figures tend to be influenced by the generally smaller clutches that are

laid late in the season by renesting females but also there may be considerable geographic variation in the average sizes of first clutches in various parts of the range. Thus, clutch size figures for the gray partridge in England differ considerably from those in North America, and data for the white-tailed ptarmigan from Montana are quite different from observations made in Alaska. Nonetheless, since information on average clutch sizes is of such basic importance in the calculation of reproductive potentials of these species, a summary of published information on clutch sizes is provided (table 12). Among the grouse the smallest average clutch sizes occur among the ptarmigan and the coniferous-forest-dwelling species, while the ruffed grouse and the prairie- and grassland-dwelling species of *Tympanuchus* have clutch sizes of about a dozen eggs. Interestingly, the sage grouse falls closer to the species of *Dendragapus* in its average clutch size (and also in the appearance of its eggs) than it does to the prairie grouse. Clutch sizes among the quail species appear to be generally high, although the limited information on tropical-forest-dwelling genera such as *Dendrortyx*, *Odontophorus*, and *Dactylortyx* suggests that these species may have quite small average clutch sizes. Among the genera *Colinus* and *Callipepla*, the combined weight of the eggs in an average clutch often nearly reaches that of the female (table 8), thus these quails expend a relatively greater amount of energy in completing a clutch than do any of the grouse.

EGG HATCHABILITY AND HATCHING SUCCESS

All available evidence from field studies indicates that the incidence of infertility and embryonic death is probably so low among wild populations as to be almost insignificant. The most extensive observations available for any grouse species are those of Bump et al. (1947), which include data from over five thousand ruffed grouse eggs, while Stoddard (1931) provides information for the bobwhite on nearly three thousand eggs from nests found in the wild. These and other studies indicate that in general more than 90 percent of the eggs laid under these conditions are fertile and capable of hatching (table 13). The actual percentage of eggs which hatch, however, is invariably less, ranging from about 90 percent to as little as 15 or 20 percent, depending on the rate of nest desertion and predation. Substantial brood mortality usually occurs during the first month or so, further reducing reproductive success (table 14).

TABLE 12

Reported Clutch Sizes under Natural Conditions

Species	Normal Range	Mean Clutch Size	References
Sage grouse	7–13	7.39 (154 nests)	Patterson, 1952
Blue grouse	6–12	6.3 (51 nests)	Zwickel & Bendell, 1967
Spruce grouse	7–10	5.8 (39 nests)	Tufts, 1961
Willow ptarmigan	2–15	7.1 (Scotland, 395 nests)	Jenkins, Watson, & Miller, 1963
		10.2 (Newfoundland, 106 nests)	Bergerud, 1970b
Rock ptarmigan	3–11	7.0 (Alaska, 101 nests)	Weeden, 1965b
		6.6 (Scotland, 148 nests)	Watson, 1965
White-tailed ptarmigan	3–9	5.2 (11 nests)	Choate, 1963
Ruffed grouse	6–15	11.5 (1473 nests)	Bump et al., 1947
Sharp-tailed grouse	5–17	12.1 (36 nests)	Hamerstrom, 1939
Greater prairie chicken	5–17	12.0 (66 nests)	Hamerstrom, 1939
Lesser prairie chicken	6–13	10.7 (7 nests)	Copelin, 1963
Long-tailed tree quail	3–6	. . . . . .	Rowley, 1966
Mountain quail	6–15	10.0 (11 nests)	P. R. Quart.†
Scaled quail	5–22	12.7 (39 nests)	Schemnitz, 1961
Elegant quail	8–12	. . . . . .	Leopold, 1959
Gambel quail	6–19	12.3 (40 nests)*	Gorsuch, 1934
California quail	9–17	13.7 (16 nests)	Lewin, 1963
Bobwhite	7–28	14.4 (394 nests)	Stoddard, 1931
Harlequin quail	6–16	11.1 (24 nests)	Leopold & McCabe, 1957
Gray partridge	9–20	16.4 (470 nests)	McCabe & Hawkins, 1946
Chukar partridge	14–19	15.5 (4 nests)	Mackie & Buechner, 1963

*Calculated, excluding four obviously incomplete clutches.
†*Pittman-Robertson Quarterly* 8 (1948):10.

TABLE 13

Egg Hatchability and Hatching Success under Natural Conditions

Species	Hatchability of Eggs	Percentage of Nests Hatching	References
Sage grouse	. . . . . .	42.2% of 533 nests	Hickey, 1955
Blue grouse	ca. 98% of eggs in 36 nests*	75% of 36 nests	Bendell, 1955a
Willow ptarmigan (red grouse)	84% of 2,464 eggs*	69% of 232 nests	Hickey, 1955
		80.3% of 395 nests*	Jenkins, Watson & Miller, 1963
Rock ptarmigan	90% of 147 eggs (Scotland)	. . . . . .	Watson, 1965
	94% of 393 eggs (Alaska)	65% of 86 nests	Weeden, 1965a
White-tailed ptarmigan	. . . . . .	70% of 11 nests	Choate, 1963
Ruffed grouse	95.6% of 5,392 eggs (1st nests)*		Bump et al., 1947
	92% of 480 eggs (2nd nests)*	61.4% of 1,431 nests	
Sharp-tailed grouse	88.2% of 136 eggs*	40% of 176 nests	Ammann, 1957
Greater prairie chicken	90.9% of 343 eggs*	46% of 165 nests	Ammann, 1957
Mountain quail	95.8% of 82 eggs	57% of 14 nests	P.R. Quart.†
Scaled quail	90% of eggs in 6 nests	14.3% of 42 nests	Schemnitz, 1961
California quail	. . . . . .	24.8% of 83 nests	Glading, 1938b
Gambel quail	. . . . . .	24% of 44 nests	Gorsuch, 1934
Bobwhite	86% of 2,874 eggs	36% of 602 nests	Stoddard, 1931
Gray partridge	84.5% of 1,838 eggs	32% of 435 nests	McCabe & Hawkins, 1946
Chukar partridge	. . . . . .	25% of 16 nests	Harper, Harry, & Bailey, 1958

*Calculated from data presented by authors
†Pittman-Robertson Quarterly 8 (1948):10.

TABLE 14

Estimates of Early Brood Mortality under Natural Conditions

Species	Mortality Estimates	References
Sage grouse	From 32 to 54% less reported in three studies	Hickey, 1955
	Average brood size reduced from 5.56 in June to 2.33 by August (48% brood loss)	Keller (in Rogers, 1964)
Blue grouse	Estimated 67% brood mortality by August	Bendell, 1955a
Willow ptarmigan (red grouse)	Average 52% of young from successful nests reared to August (48% brood mortality)	Jenkins, Watson, & Miller, 1963
Rock ptarmigan	Average 20.2% brood loss among 208 broods by late July	Weeden, 1965a
	Average brood size reduced to 3.6 young at 10-12 weeks	Watson, 1965
White-tailed ptarmigan	Approximate 33.1% brood loss among 41 broods in 1st 8 weeks	Choate, 1963
Ruffed grouse	Average brood mortality averaged from 60.9% (11 yr. avg.) to 63.2% (13 yr. avg.) in two areas	Bump et al., 1947
Sharp-tailed grouse	Average brood size reduced from 8.7 to 4.6 young (47% loss)	Hart, Lee, & Low, 1952
Greater prairie chicken	Average brood size reduced from 8.0 to 6.6 young (17.5% loss)	Baker, 1953
	Brood mortality of 46%	Yeatter, 1943
Attwater prairie chicken	Approximate 50% mortality in 1st month; 12% later	Lehmann, 1941
Mountain quail	Approximate 30% (range 0-55%) brood loss over 3 years	Edminster, 1954
California quail	Approximately 45-60% brood mortality by fall	Edminster, 1954
Gambel quail	Average 48% brood loss (range 42-51%) over three years	Edminster, 1954
Bobwhite	Approximately 25-40% brood loss in 16 weeks	Edminster, 1954
	Brood mortality 28.6% in 1st 8 weeks	Klimstra, 1950b
Gray partridge	Average brood size reduced from 12 to 8 by September (33% loss)	Yeatter, 1935

THE EVOLUTIONARY SIGNIFICANCE OF
CLUTCH SIZE VARIATIONS

The question of the adaptive significance of the considerable variations in average clutch sizes for the species under consideration here (from about five to sixteen eggs) has recently been discussed by Lack (1968). He concluded that average clutch size in these species is generally inversely related to egg size; that is, species that have relatively small clutches typically lay relatively large eggs. The apparent advantage, for species with precocial young, of producing large eggs is that the young can be hatched at a relatively advanced and less vulnerable stage and can begin feeding for themselves and soon become independent of the parent. In this group, therefore, natural selection has seemingly compromised between allowing the largest clutch size that can be produced by the energy reserves of the female while retaining an adequate egg size that will allow the young to be hatched at a stage sufficiently advanced to favor their survival.

Assuming that natural selection fixes a relatively inflexible optimum egg size for each species (which can conveniently be estimated as the weight of the egg in proportion to the adult female's weight), the physiological drain on a laying female may thus be regarded as this constant multiplied by the average clutch size. It should also be noted that among all birds, smaller species tend to lay relatively larger eggs than do larger ones, apparently reflecting the minimal investment of energy needed to produce a viable egg. Lack (1968) believes that average clutch size in the gallinaceous birds must therefore be limited either by the number of eggs that the incubating bird can effectively cover, which he rejects, or by the average food reserves of the female as modified by the relative egg size. He suggests that the latter explanation best accounts for the variations in clutch sizes to be found in this group.

Lack makes a number of additional observations about clutch sizes in the pheasant-like birds. First, he notes that clutch sizes tend to be smaller in southern than in more northerly latitudes among related species; thus tropical forms are more likely to have smaller average clutches than are related species of the same size breeding in temperate or arctic regions. Second, Lack detected no clear correlation between clutch size and habitat of the species or the pair-bond characteristics of the species. He noted that only a weak positive correlation exists between egg size and incubation period, but did not consider other possible influences on incubation periods existing in this group, such as the length of the breeding season.

As may be noted in table 8, there is only a weak inverse relationship between the average weight of the egg in proportion to that of the female

and the average clutch size in the species under consideration here. This trend is perhaps clearest in the grouse, of which the spruce grouse, rock ptarmigan, and white-tailed ptarmigan tend to have small average clutches and fairly large relative egg sizes, whereas the ruffed grouse, sharp-tailed grouse, and two prairie chicken forms have large clutches and smaller relative egg sizes. It is of interest, however, that the three ptarmigan species lay eggs of nearly the same size and that their average clutch sizes are nearly the same although they have markedly different adult weights. One would have expected that the willow ptarmigan might have a considerably larger average clutch size than the white-tailed ptarmigan.

The anticipated inverse relationship between egg size and clutch size breaks down completely in the New World quails; indeed, a positive relationship between these factors would seem to exist in this group, with the mountain quail and harlequin quail representing a small clutch–small egg condition and the California quail and bobwhite representing an opposite large clutch–large egg situation. The quail group as a whole, which on the average are smaller in body size than the grouse, rather surprisingly not only have relatively larger eggs, as might be expected from their average body sizes, but also have considerably larger average clutch sizes than do the North American grouse. This trend is clearly counter to the suggestion that egg size and clutch size characteristics are inversely related in these species.

If no strong case can be made for food reserves of the female as a major factor possibly limiting clutch size, alternate or supplementary factors must be considered. One possibility, that the clutch size is limited by the number of eggs that the adult can effectively incubate, is unpromising inasmuch as the large-bodied grouse typically produce smaller clutches than do most of the much smaller quail. It might be noted, however, that the grouse must cover their eggs more effectively, since they are mostly cool-temperate to subarctic breeders, whereas the breeding distributions of quails are more southerly and their eggs are less likely to be chilled during incubation. It seems unlikely that a ptarmigan could effectively incubate a dozen or more eggs, and each day that is invested in producing another egg not only reduces the time available for incubation and rearing of the young but also exposes the untended nest to possible predation that much longer.

If indeed the length of the breeding season is significant, and if the danger of chilling the eggs increases when the clutch size exceeds a number related to the size of the adult in proportion to the egg, then average clutch sizes should increase as breeding distributions are arranged from arctic or alpine areas to warmer ones, rather than the opposite as Lack has suggested. It

is difficult to pick representative figures on frost-free periods for the habitats of the species in question, but it might be argued that among the grouse the species might be arranged in a northerly, or alpine, to southerly, or warm-temperate, series as follows: White-tailed ptarmigan, rock ptarmigan, willow ptarmigan, spruce grouse, blue grouse, ruffed grouse, sharp-tailed grouse, sage grouse, pinnated grouse. Except for the sage grouse, which commonly breeds in parts of Utah, Nevada, and Wyoming that have frost-free seasons of one hundred days or less, this series closely agrees with a progressively increasing average clutch size. It is unfortunate that clutch size data from different populations of widely ranging species, for example, from Alaskan compared with midwestern races of ruffed grouse and sharp-tailed grouse, are not available to show if any intraspecific north-south trends can be detected in the average clutch sizes of these forms.

Since nearly all of the species of quail breed sufficiently far south that the length of the breeding season is probably not a significant factor affecting their clutch sizes, it would seem that some other factor, such as food reserves or predation effects, might play a role. Provided that adequate food is available, it is quite evident, from studies of captive quail, that females can continue to lay eggs at approximate day-and-a-half intervals almost indefinitely. Instead, the factors limiting clutch sizes in these species might perhaps be the maximum number of eggs that the adult can effectively incubate or the increasing dangers of losing the entire clutch to predators during every day that the nest is left untended during the egg-laying period. Thus, an average clutch of from ten to fifteen eggs may require about twenty days to complete, and with each passing day the possibility of their discovery by predators is increased. Lack has dismissed the possibility that predation can effectively limit clutch sizes in birds, pointing out that for it to be fully effective the predation rate must exceed the rate of laying, or approximate nearly one egg per day. Yet, since predators usually destroy entire clutches or at least often cause desertion of the nest, they may become equally effective whenever the daily likelihood of predation exceeds the inverse of the then existing clutch size. As clutch size increases, fixed daily predation levels therefore become increasingly effective as a potential limiting factor, especially for species that are relatively defenseless or do not attempt to guard the nest prior to the start of incubation.

In figure 12 are presented the calculated effects of various daily predation levels on species that lay one egg per day, assuming a constant daily predation rate during the egg-laying period causing destruction or desertion of the entire clutch. For species that average a two-day interval between eggs, the indicated effects would be doubled (thus a 5 percent daily predation rate would have the effect of the 10 percent rate shown in the figure). The

diagram demonstrates that species suffering a 20 percent daily predation level (20 percent of all initiated nests being destroyed each day) cannot effectively increase their clutch size after the third day of laying, and selection would thus favor the evolution of a clutch size of only three or four eggs. Similarly, those species exposed to a 10 percent daily predation loss cannot increase their effective clutch size beyond the eighth day. Species having a predation level of 5 percent per day can increase their effective clutch size only through the fourteenth to eighteenth day of laying, after which it levels off at eight eggs. Predation levels of less than 2 percent per day during egg laying are probably ineffective in keeping clutch sizes below the physiological limits of the female or the maximum number that can effectively be incubated, at least among species that lay an average of one egg per day.

Almost no field data on preincubation predation levels are available, but the high over-all incidence of quail nest losses through predation suggests that such losses may often reach significant levels. Since the completion of a clutch may require about twenty days, and incubation another twenty-one to twenty-four days, it follows that nearly half of all predation losses might be expected to occur before the start of incubation even if predation rates are not appreciably higher during the preincubation period. Edminster (1954) summarized field data from bobwhites and California quail indicating that some 60 to 80 percent of their nests are normally lost because of desertion or actual predation; if half of these losses occurred during the egg-laying period, it is clear that they might average at least 2 percent per day.

Stoddard (1931) reported that 37 percent of 602 bobwhite nests were destroyed by natural enemies and that 52 of the 65 nests lost to skunks were broken up before incubation started. Bump et al. (1947) found that 38.6 percent of 1,431 ruffed grouse nests were broken up, 89 percent of the disruption attributable to predators. Six studies summarized by Gill (1966) provide nest destruction estimates on 503 sage grouse nests, which averaged 47.7 percent losses (with a range of 26 to 76 percent). Recently, Ricklefs (1969) has calculated daily natural nest mortality rates for a number of North American game birds from data summarized by Hickey (1955) (see chapter 6). These calculated nest mortality rates for fifteen studies averaged 2.96 percent per day (with a range of 1.55 to 4.66 percent), which admittedly represents a minimal estimate, since the estimates are based on the entire nesting period (egg-laying plus incubation), whereas most nests are not found until the nesting period is partly over. If, in addition, it is true that in galliforms the mortality rates from predation are higher before incubation begins than afterwards, it is clear that such preincubation predation rates might have a significant role in influencing clutch size.
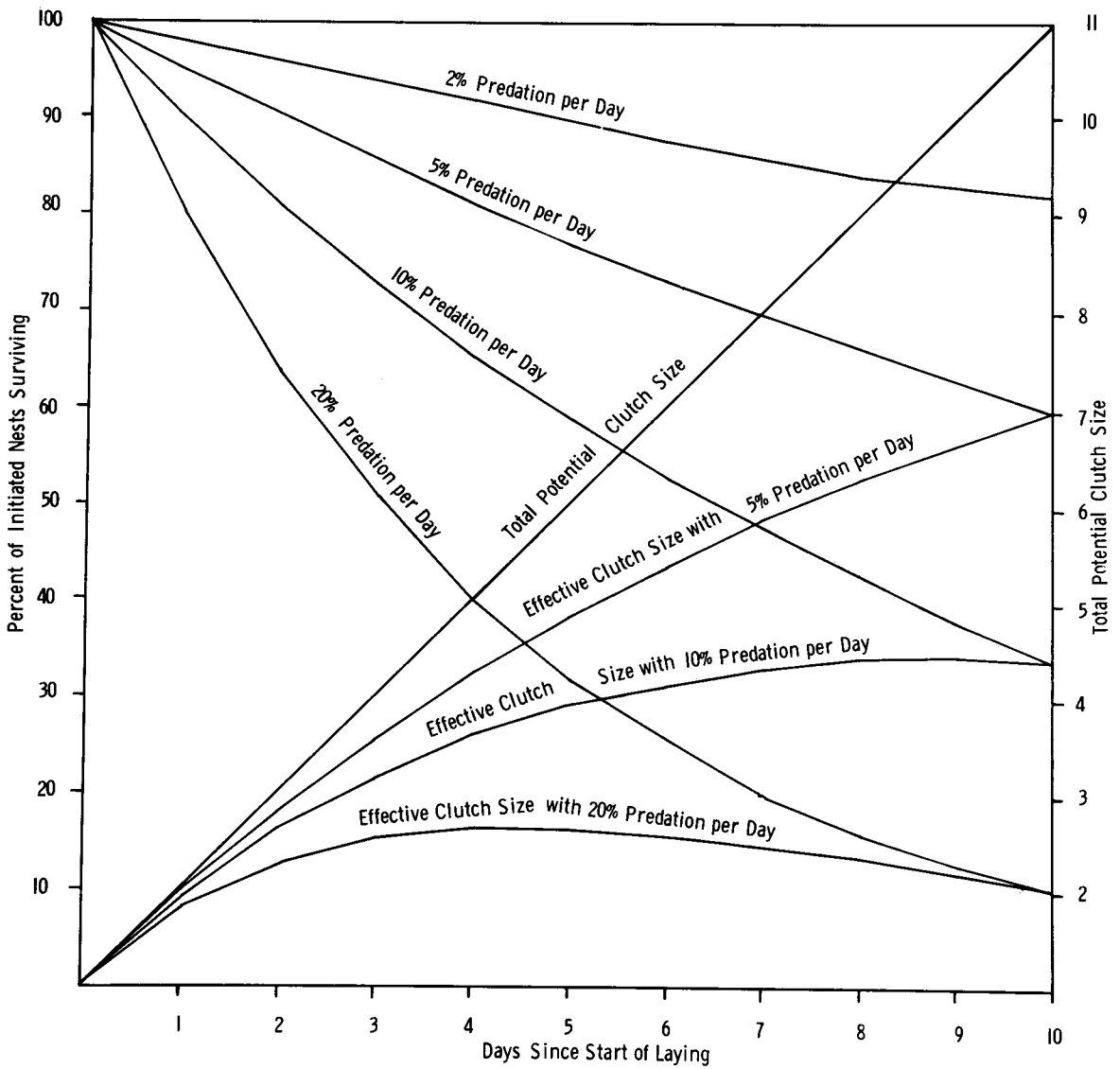
FIGURE 12. Theoretical effects of varying predation levels during the egg-laying period on effective clutch sizes, assuming an egg-laying rate of one per day and predation of the entire available clutch.

In summary, it would seem that available food reserves of the female probably play a subordinate role in limiting clutch sizes among grouse and quails and are probably important only among species that lay eggs so large or lay them so frequently that the female is unable to balance food intake against the physiological drain on her energy reserves. Otherwise the remarkably large clutches of quails and their persistent renesting behavior could not be accounted for. Among grouse, it is suggested that the need to complete a clutch rapidly and to lay no more eggs than can effectively be warmed by the female represents a significant factor in limiting clutch sizes of arctic- or alpine-breeding species, and is progressively less important for the more temperate-breeding forms. Limiting factors affecting clutch sizes of temperate-breeding species of grouse and quail might be related to the number of eggs that an adult can effectively incubate and to the predation levels during the relatively long egg-laying period, both of which would tend to allow fairly large rather than relatively small clutch sizes. It should finally be noted that the few tropical-forest-dwelling species of quail which have so far been studied appear to have quite small clutch sizes, suggesting that other limiting factors may play important roles under such ecological conditions. These factors might include relative food availability and predation rates, since Ricklefs's studies (1969) indicate that daily nest mortality rates of open-nesting passerine birds are higher in the humid tropical regions than in arctic, temperate, or arid-tropical areas; and ground-nesting quails might be similarly affected.