Life History Tradeoffs in Avian Clutch Size: Interpreting Life History Data and Evaluating Alternative Hypotheses

Jon Hess

Introduction and Background

There are strong connections across ecology, life history theory, and population biology, although they may not be obvious at first. In earlier chapters, we have talked about the fact that, in any environment, individuals with different "strategies" may not all survive and reproduce equally well. That might seem like a simple statement—but it has powerful implications for competition theory, and for population ecology. You will find, not only in this chapter but throughout this book, examples in which selection acts on clutch size (or foraging efficiency, or some other characteristic). “Best” clutch sizes (or foraging strategies, etc.) are those that result in enhanced survivorship and/or reproduction. But how do we discover these strategies?

Begin at what seems like the simplest level, and ask: if differential reproduction is key to “winning” the selective race, why doesn’t every individual, every time, make the maximum number of offspring it possibly can, in physiological terms? This is a question that has occupied scholars for some time. In life history terms, the answer is constrained optimization or tradeoffs. What any individual spends on mating it cannot spend on parenting; what it spends on either mating or parenting (together called reproductive effort) it cannot spend on keeping itself alive, growing, or any other maintenance activity (called collectively somatic effort). In any particular environment, there is some optimal strategy, given the tradeoffs. So, if we understand and can measure these tradeoffs, we can, for example, calculate the optimum age at first reproduction and the optimum clutch or litter size, and solve other life history problems (e.g., Stearns, 1992; Roff, 1992, 2003).

But the implications do not stop there. These tradeoffs vary not only across species (interspecific competition), but across populations within a species, and across individuals within a population (intraspecific competition). If we can understand these tradeoffs, we can answer important questions at several levels. A classic examination of this sort was done by British ornithologist David Lack in the 1950s. Why was it, he asked, that if you observed the same population of birds across time, the average clutch size changed from year to year? Same population, same environment—or was it? Similarly, although for simplicity’s sake we often talk as though patterns were “species typical,” Lack found variation across and within populations. So variation can include interspecific, intraspecific, and intrapopulational effects. The good news is that variation is patterned, rather than random.

At that time, many biologists held to a (somewhat illogical) view that individuals behaved in ways that benefited the species; for example, that populations “regulated” themselves.
Before you go on, think about the definition of natural selection, and see if you can understand the logical fallacy in this assumption. It is rather subtle, because many traits that help individuals survive and reproduce also have a positive impact on, for example, population growth—so they are “good” for both the individuals and the species, and it would be easy to confuse the level at which selections acts. But reproductive patterns can highlight areas of conflict. In particular, Wynne-Edwards (1962) imagined that, if an individual did not reproduce at its physiological maximum every time, it must be paying an individual cost, in order to “regulate” the population (which he saw as good at the species level). A moment’s reflection will probably convince you that there are many conditions (poor food year, a young still-growing mother) under which making the maximum possible number of offspring is not reproductively profitable. This important relationship, misunderstood by Wynne-Edwards, was one Lack studied: the nonrandom nature of variation in reproductive patterns. In a very poor resource year, is it reproductively profitable for a female bird to lay a large clutch? Most or all of the chicks will die—and she has spent her reproductive investment for nothing.

Lack did a series of now classic studies on a variety of these questions. For example, he studied nesting in the Great Tit (a British relative of the American chickadee that nests in birdhouses and is easy to study). He tested the hypothesis that clutch size is a life history trait that is under selection on the individual, as individuals compete for resources. If that is true, there may be a different “best” clutch size in good years (ample food and nest sites) and bad years, and for younger versus older birds, for example.

Objectives of This Exercise

In this exercise you will:

- Examine the variation in average clutch size across bird species
- Explore why, within species, there is usually a narrow range of variation around the average clutch size.
- Propose and evaluate alternate hypotheses about life history strategies by interpreting data
- Plot the data to help you identify trends more easily

Case Studies and Data

What factors determine clutch size? Read the following descriptions of five different species, looking first at questions 1–4 for guidance. Complete table 4.1 as you read in order to answer the questions before class.

Common Flicker Colaptes auratus (Figure 4.1)

Common Flickers (Colaptes auratus) are ground-foraging woodpeckers distributed across all of North America, and locally abundant. They inhabit wooded regions, including the giant cactus forests of the Sonoran Desert, and Baja, California. The form seen in the northern and eastern United States is called the Yellow- Shafted Flicker; the western form is called the Red- Shafted Flicker. A “hybrid zone” runs along the rain shadow of the Rocky Mountains; this has been studied for more than a century by evolutionary biologists and ecologists
TABLE 4.1.
Life history comparison of five avian species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Age first breeding</th>
<th>Longevity</th>
<th>Diet</th>
<th>Mating</th>
<th>Parental care</th>
<th>Clutch size</th>
<th>Precocial young?</th>
<th>Incubation time (days)</th>
<th>Time to fledge</th>
<th>Territorial</th>
<th>Migration</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colaptes auratus auratus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pica pica</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aix sponsa</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Perdix perdix</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parus major</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

(Moore, 1995). Flickers are monogamous and share parental care. Their eggs are lustrous white. Egg laying begins shortly after the nest is completed. One egg is laid per day, until the average clutch size of around 6–7 eggs is complete. Eggs are incubated for approximately 11 days. Young are nidicolous ("helpless"), and are fed by both parents’ regurgitation. The hatchlings subsist mainly on ant larvae. Fledglings leave the nest about 24–27 days after hatching. The young begin to breed at 1 year of age. Once an adult has bred at a locale, it returns to that locale in subsequent breeding seasons. Maximum reported longevity is 9 years and 2 months. The flickers’ predators are several species of hawk, which take both adults and fledglings (Moore, 1995).

Common Flickers use a range of habitats: open woodlands, savannas, and forest edges. They specialize in eating ants and beetle larvae, but switch to berries during late autumn, winter, and early spring. Flickers forage for ants and other insects by probing and hammering soils with their bills. Like all woodpeckers, they have protrusile tongues; their tongues can extend as much as 4 cm beyond the bill tip as they lap up adult and larval ants. During the breeding season, birds forage singly; one member of a pair is usually at or near the nest. In winter, they sometimes forage in small flocks feeding on fruit (Moore, 1995).

Common Flickers have a complex array of vocalizations, drumming, and tapping that are used in communication. They use a “long call” for territorial defense and courtship. Both sexes may aggressively defend both breeding territories and mates. These woodpeckers defend a small area around their nest tree, but have ranges that extend beyond that for foraging. These ranges have flexible boundaries, and ranges may overlap (Moore, 1995).

FIGURE 4.1. Yellow-Shafted Flicker Colaptes auratus auratus.
Most Yellow- Shafted Flicker populations (the eastern form) are migratory, funneling into the southeastern United States in late autumn, and returning to northern breeding areas in late March to early April. Southern populations are sedentary. Yellow- Shafted Flickers migrate in loose flocks that vary in size from a few individuals to more than 100 individuals (Moore, 1995).

Black- Billed Magpie Pica pica (Figure 4.2)

This bird drew attention from Native Americans because it often followed bison-hunting groups and lived on the remains of the hunts. Twelve subspecies of magpies exist throughout northern Europe and Asia. Their distribution covers much of Europe, from the British Isles, Scandinavia, northern Russia, and central Siberia south to the Mediterranean region and into northwestern Africa. Their ranges extend east to Iran, the Himalayas, southeastern Asia, China, Formosa, Korea, and Japan as well as North America, where the birds probably crossed via the Bering Land Bridge. In North America, Magpie distributions remain primarily in the central western and northwestern United States (Trost, 1999). Of the two North American magpies, the black- billed magpie (Pica pica) is the more common and widespread.

During the nonbreeding season, magpies associate with human habitats: livestock feedlots, barnyards, landfills, sewage lagoons, and grain elevators. They are generally not migratory in North America. Their habitats in the breeding season consist mainly of thickets in riparian areas often associated with open meadows, grasslands, or sagebrush for foraging. Their long tails and slow flight make it advantageous for them to keep near cover to avoid raptors (Trost, 1999).

Magpies are opportunistic, omnivorous feeders, eating ground-dwelling arthropods, seeds, and carrion; they frequently eat fly maggots rather than the meat on which maggots live. Magpie individuals observe predators, and other magpies, to learn of potential food sources.

FIGURE 4.2. Black- Billed Magpie Pica pica.
Magpies cache their food and have well-developed olfactory abilities to recover caches, enabling them to steal each other's caches (Trost, 1999). Magpies have a symbiotic relationship with large ungulates (including domestic species): they clean ticks and other ectoparasites from them. However, their relationship with moose may not be mutualistic. In Alberta, when magpies land on moose to feed on winter ticks, they tend to cache these ticks on bare ground. Most ticks live through this caching process. If ticks are not recovered later by magpies, they can survive to lay eggs, potentially increasing future numbers of ticks. Many moose die each spring from blood loss and other tick-related problems, and magpies scavenge their carcasses.

Magpies have a harsh-sounding vocal repertoire. Territoriality mainly involves silent treetop sitting, which denotes ownership of space. Magpies are quite conspicuous, with white flanks and black rumps. Nests can be dispersed, or approach coloniality when food is available. In Europe, magpies are more evenly spaced than in the Americas, and they maintain traditional year-round territories (Trost 1999).

Their mating system is monogamous; some pair for life. The maximum life span is reported to be 15 years and 1 month. The mean life span for males is 3.5 years; for females it is two years. Most females begin mating at one year; however, males are usually older than a year when they begin mating. Their eggs are tan or olive brown speckled. Clutch sizes typically range from one to nine eggs. Only females incubate; males feed their mates. Eggs hatch after about 18 days. These ridiculous young fledge 24 to 30 days after hatching, leaving the nest on average 27.5 days after hatching.

Competition among nestlings for food can lead to nestling mortality; in some cases competition intensifies into sibling cannibalism. A female may eat her eggs or small young if she is faced with human disturbance at the nest. However, starvation (both direct and indirect) is the most common cause of mortality in magpies. Underweight young are much more likely to disappear than those of average or greater weight. Chicks in broods in high-quality territories, where chicks do not beg too loudly for food (Trost, 1999), suffer less predation (especially by carrion crows) than others.

Magpies have a curious social behavior that is still not well understood. They conduct "funerals" around a dead magpie. The one to discover the dead magpie begins calling excitedly, attracting more magpies, which perch in trees, calling loudly. Up to 40 individuals may gather. Some magpies will walk around the corpse, pecking at its wings or tail. The event lasts for 10–15 minutes before all participants fly off (Trost, 1999).

**Wood Duck Aix sponsa (Figure 4.3)**

This bird is a common species in riparian habitats, wooded swamps, and freshwater marshes. Wood Ducks were very abundant across North America until the late nineteenth century, when populations declined due to the expansion of cities, overharvesting, deforestation, and destruction of wetlands. The Migratory Bird Treaty Act of 1918 protected Wood Ducks from legal harvest in the United States and Canada, and populations increased steadily, leveling off in 1985. In winter, Wood Ducks from the Canadian–United States border migrate south to southern states and into northern Mexico. Wood Ducks move in small flocks (6–12 individuals), flying mostly at night. Northeastern U.S. Wood Duck populations may travel more than 1000 km to main wintering areas; from the southeastern United States, they may travel less than 500 km (Hepp and Bellrose, 1995).

The extensive distribution of streams in the eastern United States creates the single most important habitat for Wood Ducks during the breeding season. It is essential that abundant
plant and invertebrate food sources are close to suitable nest sites. Wood Ducks are omnivorous; they eat seeds, fruits, and aquatic and terrestrial invertebrates. Where wetland food is scarce, ducks may seek acorns in upland groves, nuts in orchards, and grains in harvested fields. Immediately before and during egg laying, females eat invertebrates rich in protein and calcium, which are essential for egg production (Hepp and Bellrose, 1995).

Wood Ducks are socially monogamous—they have only one mate at a time. However, because males do not help care for the young, they are sometimes serially monogamous (polygynous). A female’s age at first reproduction varies by region. In South Carolina, 82% of females reproduce after one year of age, but in Massachusetts only 58% of females reproduce that early, probably reflecting differences in a number of costs (food availability, costs of migration, length of “good season”). The mean survival rate to 20 years of age is 0.56 for males and 0.51 for females.

Tree cavities provide the main nesting sites for Wood Ducks. The female lays 11–23 white glossy eggs. Incubation takes 25–37 days (average=28.8 days). Once the chicks in the eggs begin “piping” (pecking at the shell from inside), the female rarely leaves the nest unless disturbed. Ducklings usually leave the nest in the morning about 24 hours after hatching. When the coast is clear, the female flies from the nest cavity to the ground or water below, and begins calling softly. Ducklings immediately climb to the entrance and leap from the nest to the female. They are not assisted in any way, and have been reported to make spectacular jumps (up to 9 m to the ground) without injury. Obviously, these chicks are precocial. Associations between young and adults may last up to 8 weeks. When they are able to fly, the young disperse short distances (0.3–10.8 km); males go further than females (Hepp and Bellrose, 1995).

Eggs are eaten by rat snakes, raccoons, fox squirrels, mink, and various woodpeckers, including the Northern Flicker. Young ducklings are eaten by Great Horned Owls, mink, snapping turtles, bullfrogs, large predaceous fish, and alligators. Adults are vulnerable to owls, mink, raccoons, and alligators, as well as red and gray foxes. Females flush from the nest at any disturbance. Ducklings respond to the female alarm calls by skittering across
the water to cover while the female swims in a different direction or feigns a broken wing. Both adults and young are excellent swimmers and will occasionally dive for food to depths of up to 1 meter. Young birds can sometimes escape predators by diving (Hepp and Bellrose, 1995).

Wood Ducks are not territorial, but males will defend mates when approached too closely; this results in a small moving territory. Wood Ducks’ lack of territoriality is suggested to be an adaptation, because they breed in habitats with fluctuating water levels, where temporal and spatial distribution of food varies. There are no feeding territories in the fall or spring; pairs of birds feed close together without aggressive interaction (Hepp and Bellrose, 1995).

**Partridge Perdix perdix (Figure 4.4)**

Partridges are found in cool mid-latitude lowlands, and in temperate and steppe zones, penetrating into boreal zones and the Mediterranean. The Partridge is strictly a ground bird, preferring continuous grass or brush no higher than its head. It also seeks access to bare dusty ground, fallows, ploughed land, or dunes. Its distribution extends from the British Isles to Denmark, through Norway, Sweden, Finland, and the western part of the former Soviet Union, north into Russia. Italy and Portugal also have populations (Cramp et al., 1980), and it has been introduced into northern North America. The Partridge is mainly a “resident” bird, but some populations in Eastern Europe migrate. Diet consists chiefly of plant materials; but partridges occasionally eat insects (mostly females, when feeding chicks). Partridges are crepuscular, foraging soon after dawn and before sunset. Partridges live in flocks for 7–8 months of the year (July/early August until January or February); in the breeding season they form pairs to mate and raise chicks.

Flocks usually comprise 5–15 individuals, but may sometimes be as large as 20–25. Flocks remain within their home ranges that are greatly overlapping. Flocks tolerate each other, so each flock has a moving territory surrounding it. When birds are numerous and food is short, tolerance increases, allowing flocks to get closer, but flocks do not mix. Sometimes when flocks approach each other, old males perform threat displays for up to five minutes. When agitated, birds in the flock jump and flutter their wings. Subsequent attacks

![Figure 4.4: Partridge Perdix perdix.](image)
may occur spontaneously, or may be provoked by sudden movements in the other covey. The attacks lead to chases, and to gradual separation of the groups involved. Up to 50 birds may chase each other, apparently indiscriminately, over a small area. Aggression may occur not only between members of opposing flocks, but between siblings; parents may even attack offspring. Aggression within flocks has been noted only in early autumn, when flock composition is not fully stabilized (Cramp 1980).

When two flocks converge, pairs may form. There is a sudden turmoil of aggressive and sexual interaction; males fight to assert dominance over other males, and females over other females. In the end, males and females form socially monogamous pairs. These pairs commonly reunite in subsequent seasons. In Britain, eggs are laid in late April and early May. Nests are on the ground in thick vegetation. The eggs are olive-brown, smooth and glossy. Mean clutch size is 14.6 in England and 18.3 in Finland. Incubation takes from 23 to 25 days (mean 24.8). Only females incubate, but males may help when eggs are hatching. Young are precocial, and largely self-feeding; however, both parents accompany the young. It takes 15 days after hatching for young to fly, though they can flutter off the ground at 10 days. The age of first breeding is 1 year and the oldest breeders are about 5 years old (Cramp 1980).

Partridges have many different vocalizations to advertise and threaten, to call to gather, and to warn of ground or aerial predators. Predation, particularly by red foxes, cats, and stoats, is one of the most important causes of prehatching mortality. Chick survival to 6 weeks is highly variable and heavily dependent on food availability (Cramp 1980).

**Great Tit Parus major (Figure 4.5)**

The Great Tit, *Parus major*, is one of the most-studied small birds in the world; its wide distribution, abundance, and readiness to nest in a box make it a convenient study species.
(McCleery and Perrins, 1988). One simply needs to inspect nest boxes to determine demographic information: the number of pairs, clutch size, and the number of young raised. The research suitability of the tit was first appreciated in Holland in 1912, and studies of the Great Tit have continued for almost a century now. Its diet consists mainly of insects, especially in the summer; but it forages for certain seeds in winter. These small birds are known for their relatively high metabolic rate; Great Tits spend about 75% of their day feeding (Barnes, 1975).

The distribution of Parus major extends from Europe far into the east, through Iran and into Mongolia. There are also scattered populations in northwestern Africa. The bird is common, diurnal, and is easily trapped and marked in the winter. In the Oxford, England, district, it is a resident all year. Adults are nonmigratory. In September the birds exhibit some territorial behavior; when it gets colder they tend to flock. Autumnal displays and fighting among Great Tits have been attributed to the advantage to young birds of establishing territories before winter. By the end of September, flocks have become stable and their ranges more clearly defined; their density is about one pair per hectare (McCleery and Perrins, 1988).

Pair formation starts at the end of January, and pairings are socially monogamous. The first clutch is usually started in April (Dhondt et al., 1996). Clutch size varies from 8 to 13 eggs (mean 9). Incubation time is 12–15 days. Only the female incubates the eggs; if the male enters the nest hole, it is usually to take food to his mate. A female will raise her wings, expand her tail, and give a most impressive hiss when disturbed while brooding her eggs (Barnes, 1975). Young are nidifugous, not nidicolous—they leave the nest. However, they are altricial, not precocial, and the female continues to brood them for a day or two after hatching because they are featherless (Barnes, 1975). Spiders and their eggs are regularly given to the nestlings; grit and crushed snails are also regular items in small quantities, presumably to aid in digestion (Barnes, 1975). If a pair’s clutch fails, they will usually renest together; if the first brood is successfully fledged, some pairs may start a second brood in the same season (Dhondt et al., 1996). Second broods within a season are rare, although lost clutches are often replaced (McCleery and Perrins, 1988).

The young fledge about 6 weeks after hatching (Dhondt et al., 1996). For two to four weeks after leaving the nest, the young move about in family parties (Barnes, 1975). In July or August the young birds typically join mixed-species flocks. In late summer and early autumn, several species of warblers (and sometimes Spotted Flycatchers and Pied Flycatchers) may temporarily join tit flocks (Barnes, 1975). Only a small proportion of the fledged young reach breeding age; more than half of those that breed do so only once (McCleery and Perrins, 1988). Average age at first breeding is a year (Clark and Linden, 1975), and mean life length is 7.8 years (Barnes, 1975).

Questions to Work on Individually Outside of Class

1. Complete table 4.1, which compares life-history traits in the five species that you read about above. Do you see patterns or possible correlations across species?

2. What aspects of avian life history might be relevant to understanding or explaining variation in average clutch size either across or within species? Do you think having precocial (or nidifugous) chicks, as opposed to altricial (or nidicolous) chicks, may affect incubation time or clutch size? Explain.
3. How does feeding behavior change in different bird species during different parts of the year? What would be some reasons for these changes? How might feeding behavior affect or be affected by breeding behavior?

4. If the size of a population is stable over time, what relationship do you expect between recruitment (birth or hatching) and mortality? How would immigration and emigration factor into this equation?

**Small-Group/In-Class Exercise**

This week you will use the time in class to answer the following questions in your group. These questions will require you to pay close attention to details, and to assess and integrate information from many different sources. Discuss each question as a group and hand in your written answers at the end of class. Natural selection predicts that the individual with the largest genetic impact on a population will be the one that leaves the most offspring that are in turn reproductively successful. It follows that a population would quickly become dominated by individuals that leave the greatest number of reproductively successful offspring. So is it surprising when populations of birds are observed to maintain a typical clutch size that is smaller than the largest clutch size in the population? In other words, the population does not seem to be getting replaced by birds producing the greatest number of eggs. Examine the experimental data below and discuss the questions that follow in order to discover the solution to this putative paradox. The table you assembled in question 1 at home will be useful in answering many of the questions below.

5. Consider the following manipulation: A Yellow-Shafted Flicker, *Colaptes auratus*, usually lays a clutch of 6 to 8 eggs; on average one egg is laid per day. The female then incubates the whole clutch until the eggs hatch. One female laid 71 eggs in 72 days when the eggs were removed by a scientist as soon as they were laid (Phillips, 1887).

   How can you reconcile this observation with the fact that undisturbed flickers lay a maximum of 8 eggs?

6. Consider the following natural experiment:

   The most frequent clutch size of the Partridge in England is 15 eggs. The Wood Duck in Iowa most frequently has clutches of 11–14 eggs. Examine the data on hatching success in relation to clutch size in these two species (table 4.2).

   (a) You can assume that, within species, the birds sampled were all approximately the same size. What can you conclude if these data are representative and do not change much from year to year?

   (b) How would you state the hypothesis that could be tested with these data?

7. Recall the introductory discussion of costs and benefits of individuals reproducing maximally and individuals responding to ecological conditions. Wynne-Edwards (1962) attempted to explain why animals “restrain” themselves from producing more offspring than they are physiologically capable of producing in a given breeding season. He assumed that the only individually selective behavior was to make the maximum physiologically possible number of offspring. In our examples, Wynne-Edwards would have described laying as many eggs as physically possible as selfish behavior that will enhance the reproduction of the bird who lays those eggs. He explained less-than-maximum reproduction as “altruistic” restraint that avoided population crashes in the future. Such hypotheses are called “group
### Table 4.2
Fartridge and Wood Duck reproductive data.

<table>
<thead>
<tr>
<th>Clutch size</th>
<th>Total eggs</th>
<th>Percent hatched</th>
<th>Clutch size</th>
<th>Total eggs</th>
<th>Percent hatched</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>—</td>
<td>—</td>
<td>7, 8</td>
<td>7</td>
<td>86</td>
</tr>
<tr>
<td>8</td>
<td>120</td>
<td>91</td>
<td>9, 10</td>
<td>96</td>
<td>85</td>
</tr>
<tr>
<td>9</td>
<td>351</td>
<td>88</td>
<td>11, 12</td>
<td>194</td>
<td>86</td>
</tr>
<tr>
<td>10</td>
<td>1,080</td>
<td>91</td>
<td>13, 14</td>
<td>202</td>
<td>88</td>
</tr>
<tr>
<td>11</td>
<td>1,716</td>
<td>91</td>
<td>15, 16</td>
<td>124</td>
<td>82</td>
</tr>
<tr>
<td>12</td>
<td>5,340</td>
<td>90</td>
<td>17, 18</td>
<td>70</td>
<td>93</td>
</tr>
<tr>
<td>13</td>
<td>5,681</td>
<td>90</td>
<td>19, 20</td>
<td>59</td>
<td>98</td>
</tr>
<tr>
<td>14</td>
<td>9,324</td>
<td>90</td>
<td>21–25</td>
<td>116</td>
<td>26</td>
</tr>
<tr>
<td>15</td>
<td>10,650</td>
<td>91</td>
<td>Total</td>
<td>868</td>
<td>80</td>
</tr>
<tr>
<td>16</td>
<td>9,552</td>
<td>91</td>
<td>Total</td>
<td>868</td>
<td>80</td>
</tr>
<tr>
<td>17</td>
<td>6,052</td>
<td>90</td>
<td>Total</td>
<td>868</td>
<td>80</td>
</tr>
<tr>
<td>18</td>
<td>4,104</td>
<td>90</td>
<td>Total</td>
<td>868</td>
<td>80</td>
</tr>
<tr>
<td>19</td>
<td>1,520</td>
<td>91</td>
<td>Total</td>
<td>868</td>
<td>80</td>
</tr>
<tr>
<td>20</td>
<td>840</td>
<td>91</td>
<td>Total</td>
<td>868</td>
<td>80</td>
</tr>
<tr>
<td>21–29</td>
<td>831</td>
<td>92</td>
<td>Total</td>
<td>868</td>
<td>80</td>
</tr>
</tbody>
</table>

selection hypotheses because they imply that natural selection is working between groups and that characteristics that benefit the group as a whole (even if they are costly to the individual) will be favored. "For the good of the population" and "for the good of the species" explanations are used in popular literature and natural history films to explain a wide array of animal behaviors.

(a) Consider Wynne-Edward’s hypothesis. What advantage would an individual confer on other group members, if it restrained itself and laid few (or no) eggs?

(b) If a selfish individual (that lays as many eggs as possible) were to invade a group made up of restrained altruists, what would happen to the group composition in the next generation?

(c) If only one group exists, and it is composed of both selfish and altruistic individuals, could Wynne-Edward’s group selection have an impact on the composition of the group?

(d) Now consider both Wynne-Edward’s hypothesis and Lack’s alternative individual-selection hypothesis. Which hypothesis would be more useful in explaining the Partridge and Wood Duck data?

8. Consider table 4.3 (these are data on fledgling survival in Great Tits [based on Lack et al., 1957])
Table 4.3.
Survival of young Great Tits (1945–1955); mean clutch size = 9.1–10.1.

<table>
<thead>
<tr>
<th>Brood size</th>
<th>Initial number of young</th>
<th>Number alive 3 months later</th>
<th>Percentage alive 3 months later</th>
</tr>
</thead>
<tbody>
<tr>
<td>3–7</td>
<td>200</td>
<td>13</td>
<td>6.5</td>
</tr>
<tr>
<td>8</td>
<td>216</td>
<td>14</td>
<td>6.5</td>
</tr>
<tr>
<td>9</td>
<td>369</td>
<td>27</td>
<td>7.3</td>
</tr>
<tr>
<td>10</td>
<td>400</td>
<td>26</td>
<td>6.5</td>
</tr>
<tr>
<td>11</td>
<td>220</td>
<td>6</td>
<td>2.7</td>
</tr>
<tr>
<td>12–13</td>
<td>61</td>
<td>1</td>
<td>1.6</td>
</tr>
<tr>
<td>Total</td>
<td>1466</td>
<td>87</td>
<td>5.9</td>
</tr>
</tbody>
</table>

(a) What can you conclude about long- and short-term consequences of different brood sizes?
(b) How would you state the hypothesis that could be tested with these data?

9. Use the details of the next set of studies on Magpies, along with what you know of the Magpies’ natural history, to answer questions a through e. In one experiment, Magpie nestlings of 0 to 3 days old were added or removed from nests to create pairs of birds with various brood sizes (table 4.4). Reproductive Output (R.O.) is the average number of young surviving to the growth stage immediately before leaving the nest and was measured for these different brood sizes. This value is in relation to initial clutch size and the natural, or manipulated, brood size. The R.O. values are in bold for the brood sizes that correspond with the initial clutch sizes chosen by the parent birds.

In a follow up study “... clutch size variation between different birds in the same territory and the same birds in different territories indicate[d] that 81 to 86 percent of the within-years variation in Magpie clutch size is linked to differences in territories” (Högstedt 1980). In other words, different Magpie breeding pairs using the same territory in the same year had relatively low variation in their clutch sizes. In contrast, the same pairs trying out different territories in the same year had relatively high variation in their clutch sizes. Now try answering the following questions:

### TABLE 4.4.
Reproductive output (R.O.) in the Magpie.

<table>
<thead>
<tr>
<th>Initial clutch size</th>
<th>Brood size (natural and manipulated)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>4</td>
</tr>
<tr>
<td>5</td>
<td>0.3</td>
</tr>
<tr>
<td>6</td>
<td>1.7</td>
</tr>
<tr>
<td>7</td>
<td>3.5</td>
</tr>
<tr>
<td>8</td>
<td>2.5</td>
</tr>
</tbody>
</table>
TABLE 4.5.
Nestling weight and survival in the Great Tit.

<table>
<thead>
<tr>
<th>Weight (15th day) (g)</th>
<th>Number weighed</th>
<th>Number alive 3 months later</th>
<th>Percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>8.0–12.9</td>
<td>23</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>13.0</td>
<td>10</td>
<td>—</td>
<td>0</td>
</tr>
<tr>
<td>14.0</td>
<td>21</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>15.0</td>
<td>46</td>
<td>1</td>
<td>1.9</td>
</tr>
<tr>
<td>16.0</td>
<td>58</td>
<td>1</td>
<td>—</td>
</tr>
<tr>
<td>17.0</td>
<td>173</td>
<td>9</td>
<td>5.2</td>
</tr>
<tr>
<td>18.0</td>
<td>347</td>
<td>19</td>
<td>6.5</td>
</tr>
<tr>
<td>19.0</td>
<td>323</td>
<td>19</td>
<td>5.9</td>
</tr>
<tr>
<td>20.0</td>
<td>150</td>
<td>8</td>
<td>—</td>
</tr>
<tr>
<td>21.0</td>
<td>39</td>
<td>5</td>
<td>6.8</td>
</tr>
<tr>
<td>22.0</td>
<td>2</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

*Source: Based on Lack (1957).*

(a) Consider a pair of Magpie breeders that occupy a given territory. They have been feeding in that territory and begin laying eggs. Later, just as they finished hatching 5 nestlings, a mischievous ecologist adds another 2 Magpie nestlings. Given the data above, what do you predict will happen?

(b) What do the data in table 4.4 and the follow-up experiment suggest determines the Magpie’s clutch size?

(c) Which clutch size appears to yield the highest R.O. value?

(d) Why is it that all the Magpies are not laying the clutch size with the highest R.O. value?

(e) If 81–86% of the within-year variation in Magpie clutch size can be accounted for by differences in territories, what do you think causes the remaining variation?

10. Finally, let us consider the mean weight of nestlings in relation to brood size. Examine the data in table 4.5 and figure 4.6, from Perrins (1965) and Lack (1957). What is suggested by these data as yet another factor important in determining most frequent clutch size?

To answer the following questions, draw on the wide array of data and examples you have become familiar with in this exercise.

11. In a season with superabundant food resources, when there is no limit to the amount of food one can gather, what do you think would be the effect on most frequent clutch size?

12. Consider birds living on an island that is often subject to devastating hurricanes. Would natural selection favor a reproductive strategy of rapid maturation and perhaps explosive reproduction, or longer time to maturity, and repeated reproduction? For example, would you expect to find reproduction heavily concentrated in one or two seasons, or smaller clutch sizes in any one year, but reproduction across six or more seasons?
13. What are some caveats to applying the conclusions gathered from an experiment on one species to other species (or even a single experiment within one species to all populations of a species)?

14. Integrate all the evidence you have been given and think about a wide range of bird species. What general factors determine the life history tradeoffs of large-versus-small clutch size, and few-versus-many seasons of breeding? Remember that birds must trade off their own survivorship and their reproduction. For example, fewer seasons of reproduction may result in fewer offspring over the lifetime, but if life is dangerous, early reproduction may get genes into the next generation, and ultimately result in good success in grand or great-grand offspring. On the other hand, if life is relatively safe for adults, but dangerous for offspring, adults who hedge their bets by reproducing repeatedly may prosper. Assume that resources are only mildly affected but population size fluctuates widely.

References


