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Life-history strategies

- Diversity of life histories
- Power laws
- The metabolic theory of ecology
- The pioneering work of Cole and Lewontin
- The MacArthur and Wilson *r*- and *K*-selection theory
- Cost of reproduction, allocation of energy, and clutch sizes
- Predation and life histories
- The Grime model of life histories for plants

6.1 Introduction

To the uninitiated, nothing could be worse than accompanying a bunch of "birders" on a field trip. They keep stopping, peering through their binoculars, whispering to each other, and motioning you to keep quiet. Why are they so fascinated with birds? Aren't they all pretty much the same?

Of course not. Even the most naive non-biologist knows that birds come in an amazing variety of colors and sizes; amateur birders are legion. What we are interested in exploring in this chapter, however, is the variety and potential adaptive value of life histories found in all groups of organisms. Since ornithologists such as David Lack have contributed so much to our understanding of life histories, we begin by using birds to illustrate the complexity and diversity of life histories. These accounts are mostly based on Janzen (1983).

1 The groove-billed ani (*Crotophaga sulcirostris*) is a common and conspicuous bird found in the lowlands and mid-elevations of Central America. Females are about 65 g in mass, but lay extremely large 11 g eggs. Since each female may deposit 4–8 eggs in the nest, the combined total mass of her eggs may exceed her body weight. What is more extraordinary, however, is that this species engages in a communal breeding system. The birds live and breed in a group ranging from two to eight adults, with an equal number of males and females. The group defends a common territory, year-round. A single nest is

constructed and all females deposit their eggs in it, forming a communal clutch. All members of the group contribute to incubation and feeding of the nestlings. Anis are highly social, roosting and sleeping in close contact with each other while engaging in mutual grooming. However, Vehrencamp (1977, 1978) found that there are specific costs and benefits to the individuals participating in this group endeavor. For example, there are individual differences in the number of eggs that get into the nest, in the amount of time and effort put into incubation, and in the care of the nestlings. Furthermore, the eggs and offspring of the dominant females and males benefit the most. Dominant females lay their eggs last and actually remove eggs laid by other females from the nest. These dominant females then behave like brood parasites in that they actually put less effort into incubation and feeding than do the subordinate females. On the other hand, so-called alpha males, who have the most eggs in the nest (and the most to lose), perform a large share of the incubation. What is the advantage of communal nesting, especially for the subordinate birds? How do the dominant females get away with dumping the subordinates' eggs while they do less of the work?

2 The northern jacana (*Jacana spinosa*) is found from Costa Rica northward in Central America wherever there is floating aquatic vegetation. Jacanas have reversed the usual roles of the genders. Males build the nests and incubate and care for the young. Females lay one egg a day for four days in a typical clutch. Females are able to lay a second clutch of eggs elsewhere within 7 to 10 days, if necessary. The eggs are quite small (7.9 g) as compared with the average weight of the females (160.9 g). Males are smaller (mean weight of 91.4 g) than females. The mating system is polyandrous. Each male defends a small territory while each female defends a territory containing one to four males. Once chicks reach 12–16 weeks of age the females often provide a second clutch for the males to care for. The ratio of males to females varies seasonally and from place to place, but is often skewed in favor of the males. For example, the long-term average at Turrialba, Costa Rica was 2.3 males per female (Jenni 1983). Jacanas have a very high reproductive potential, but the hatching and fledging survivorship rates are very low.

3 The frigatebird (*Fregata magnificens*) is a large (800–1700 g) seabird with a life history that is unusual because of its low reproductive potential. Both sexes do not become mature until 5–8 years of age. Females breed only every other year and lay one egg in a clutch. The egg takes 55 days for incubation and the nestlings grow very slowly. They are fed primarily by the females for as long as 14 months. Given a 50 : 50 sex ratio, a new female is produced, on average, only every four years! The potential *r*-value for this species is extremely low, but by contrast survivorship of adults is very high. The life span is 40 or more years. What selective pressures resulted in a life history so radically different from that of most bird species?

4 Brown pelicans (*Pelecanus occidentalis*) are one of the best-known birds in the western hemisphere. They are found on both the Atlantic and Pacific coasts from North Carolina to Brazil and from British Columbia to Chile. Breeding colonies may contain as many as 500 pairs. An adult brown pelican weighs between 2 and 5 kg; it takes 3–5 years to attain adult plumage. Males and females share chick-raising duties equally, and the normal clutch size is three eggs. Incubation takes 30 days and the nestlings need 10–12 weeks to fledge.

Schreiber and McCoy visited a pelican colony four times during the breeding season of 1979 on Isla Guayabo in Costa Rica. Of 430 nests surveyed, most had three eggs, but the average was 2.42. By their fourth visit the number of surviving fledglings was 506, which was an average 1.18 per nest. The brown pelican is much larger than the frigatebird, has a much higher reproductive potential, but also has a lower survival rate.

5 Oropendolas (*Zarhynchus wagleri*), which are related to blackbirds and orioles, nest in colonies. Males weigh twice as much as females (212 versus 110 g) and they have been shown to take twice the energy to fledge as opposed to a female. As a result, male mortality among chicks is much higher during times of food scarcity. The sex ratio at colonies is normally 5 : 1 in favor of females. In Costa Rica, nesting begins with the dry season (December) and three complete breeding cycles are possible before the beginning of the rainy season in May. The normal clutch size is two, but breeding success is very low. The average number of chicks fledged per nest is 0.40. On the other hand, survivorship of adults is very high. Adults have been recorded living beyond the age of 26 in the field. By contrast to frigatebirds, which also have very long adult life spans, this species has a much higher reproductive potential.

So what have we learned about life histories from these birds? Nesting ranges from communal to colonial to pair-wise. Breeding systems vary from communal to polyandrous to simple pair bonds. Fecundity varies from one egg every other year to as many as eight in one clutch. Survivorship of the chicks is as low as only 0.40 per nest, but adult survivorship is as high as 40 years. What accounts for all this variation in life histories? Under what conditions do we find high versus low fecundity and/or survivorship? These are questions we want to attack in this chapter.

Another set of questions we wish to address concerns the relationship between the body size of an organism and its reproductive potential. Although body mass does not determine all aspects of life history, it is a powerful influence. For example, Fig. 6.1 is based on data for 24 species of mammals found in Costa Rica. The log of the length of the pre-reproductive period was graphed against the log of adult body mass. The obvious conclusion is that there is a higher likelihood of delay in reproductive maturity in the larger animals. Similarly, Fig. 6.2 demonstrates that animals with larger mass also have a longer interval between births. Litter size and total reproductive output per year were negatively associated with body mass, though the relationships were weak in this set of data.

Basic life-history equations were available early in the twentieth century (Lotka 1925). But a serious comparison of life-history parameters across a large number of species did not begin until 1954. In that year Frederick Smith and L.C. Cole published important papers that have become the foundation of life-history analysis.

Smith (1954) surveyed the literature and published what was known about r, R_0, and G (generation time) at that time. Using the well-known relationship:

$$N_t = N_0 \, e^{rt}$$

and setting t = the generation time, G, we have:

$$N_G = N_0 \, e^{rG} \quad \text{and} \quad \frac{N_G}{N_0} = e^{rG}$$