nothing about the fitness consequences of different individual strategies. There is great variation within a population in breeding strategies, even though one can presume that the proximate cues experienced (daylength, rainfall) are virtually identical (Figures 2.2, 2.3). In Song Wrens, *Cytororhynchus phaeocephalus*, many pairs begin breeding in May, at the start of the wet season, but other pairs did not lay their first eggs until September or October (Robinson *et al.* 2000). The unpredictability of tropical breeding seasons at the individual level is illustrated nicely by White-fronted Bee-eaters, *Merops bullockoides*, in Kenya (Wrege and Emlen 1991). Breeding colonies separated by only a few kilometers breed 6 months apart, during either the long rainy season (March–May) or the short rainy season (October–December). Within a colony, neither insect abundance nor rainfall consistently correspond with time of breeding. Even more puzzling, nests initiated during either the short rainy season fledge three times as many young as long rainy season nests. There is no obvious adaptive explanation for why adjacent colonies breed at different times of the year, but there must be one. Hypotheses developed to explain temperate zone breeding systems are inadequate for explaining this kind of tropical phenomenon.

### 3 Life history traits

It has long been recognized that tropical birds differ fundamentally from temperate zone birds in their life history traits. Tropical birds have high nest predation, high adult survival and small clutch sizes (Lack 1947, 1948, 1968, Ricklefs 1969b, Fogden 1972, Skutch 1949). These characteristics in turn have a big impact on the evolution of other behaviors such as mate choice and territory acquisition. More recent studies, however, have questioned the validity of these differences in tropical birds (Karr *et al.* 1990, Martin 1996, Geffen and Yom-Tov 2000), causing some confusion and doubt as to whether tropical birds differ importantly in life history traits. The purpose of this chapter is to review these debates and determine what life history traits characterize tropical birds. Others have carefully reviewed the evolutionary hypotheses to explain why tropical birds are different (Klomp 1970, Murray 1985, Skutch 1985), so this chapter will summarize what is known rather than attempt a comprehensive review.

#### 3.1 High nest predation

Early studies of tropical birds typically reported a high percentage of nests lost to predators, in the order of 80% or more (Snow 1962, Willis 1967, 1972, Fogden 1972, Snow and Snow 1973). In contrast, a predation frequency of 40–60% is typical of many temperate zone songbirds (Martin 1993). Some have argued that high nest predation rates in tropical birds are an artifact of habitat, because a number of the key studies were done in human-disturbed habitats or islands where predation rates may be elevated (Oniki 1979, Martin 1996). But recent studies in large mainland tracts have also found low nesting success (Robinson *et al.* 2000). Other studies that question the high nest predation rate in the tropics have used artificial nests, and found nest losses in the order of 10–50% (Loiselle and Hopps 1983, Gibbs 1991, Sieving 1992). Artificial nests often do not reflect true predation frequency (e.g. Wilson and Brittingham 1998), so these alone cannot be used as evidence for low nest predation in the tropics.
Relatively few studies provide detailed data for nest predation frequency for a large sample of nests of a particular species. A wide diversity of passerines often lose at least 70% of nests (Figure 3.1). This also applies to many non-passerines, like the Rufous-breasted Hermit, *Glaucis hirsuta* (Snow and Snow 1973) and Plain Ground Dove, *Columbina passerina* (Oniki 1979). Robinson et al. (2000) found that only 29% of open-cup nestling forest birds in Panama fledged young. Predation is the primary cause of nest failure (Ricklefs 1969b). The percentage of nests lost underestimates nest predation, because this does not take into account when the nest was first found (many early nests could have been depredated and therefore never found). Several studies also used Mayfield’s method which estimates daily mortality rate (Young 1994, Roper and Goldstein 1997, Woodworth 1997, Robinson et al. 2000). In Dusky Antbirds, *Cercomacra tyrannina*, only 8% of pairs (15/197) raised young to independence over an eight-year study, indicating that nesting success must be very low (Morton and Stutchbury 2000).

Martin (1996) notes some exceptions, tropical species with high nesting success, but these studies were based on relatively small sample sizes and are not comparable (Snow and Snow 1963, Skutch 1981).

![Image](image.png)

**Figure 3.1**

Frequency distribution of predation frequency on nests for studies on north temperate passerines (n = 25, Martin 1993) and Neotropical passerines (n = 9; Snow 1962, Morton 1971b and unpub. data, Willis 1974, Oniki 1979, Wunderle 1982, Skutch 1985, Young 1994, Roper and Goldstein 1997, Woodworth 1997). Only studies with at least 100 nests monitored were included.

Nest predation in the tropics likely varies with habitat (Marchant 1960), time of year (Morton 1971b) and possibly altitude (Skutch 1985). Although very high nest predation (> 80% nests) has been reported for several temperate zone studies (Snow and Snow 1963, Martin 1993), this is certainly not the norm except in highly disturbed habitats (e.g. Robinson et al. 1995). For temperate zone passerines the frequency of nest predation averaged 43.7% (Martin 1993), much lower than for tropical passerines (Figure 3.1). Robinson et al. (2000), using a more detailed data set, found that open cup nestling temperate zone birds averaged 47% nest loss compared with 71% for tropical birds.

While this sort of comparison is very convincing, many of the tropical species are members of groups that do not have temperate zone counterparts (antbirds, manakins). Many features of behavior and life history could influence predation frequency, so a search for real latitudinal differences owing to habitat should take phylogeny into account. This is not yet possible because so few tropical species have been studied in sufficient detail to estimate predation frequency.

A formal comparative analysis not withstanding, we can conclude that nest predation is higher for most tropical birds. Why is nest predation so high? It is generally assumed that there is a higher number and diversity of nest predators in the tropics. Skutch (1949, 1985) suggested that snakes are the primary nest predators, but other studies do not support this (Roper and Goldstein 1997). Instead, a high abundance and diversity of small mammals, such as mouse opossums, *Marmosa* sp., in the neotropics, may be implicated as the main predator species (Roper and Goldstein 1997).

### 3.2 High adult survival

Snow (1962) was one of the first to show high annual survival (70%) of adults in a tropical bird, the White-bearded Manakin, *Manacus manacus*. Fozden (1972) did not study any one species intensively, but reported that 200 of 286 (86%) banded adults of a variety of species were alive one year later. Willis (1974) reported survival rates of 69–81% for three species of antbirds in Panama, despite two of the species declining significantly over the study. Most long-term intensive studies of populations report high adult survival based on resightings and recaptures of breeders (Table 3.1, reviewed in Sandercock et al. 2000). Such high annual survival rates result in lifespans greater than 10 years being common for these small birds (Snow and Lill 1974,
Parrotlet, *Forpus passerinus* (Sandercocock et al. 2000), where survival estimates for non-territorial floaters are much lower than for territorial breeders (Figure 3.2). For many questions in behavioral ecology, we are interested in how long a breeder is likely to survive. This affects decisions about reproductive effort, mate choice and switching territories. Juvenile survival is important too, but for a different set of evolutionary questions such as how to acquire territories, and when and if to disperse.

![Figure 3.2](image-url)

**Estimates of survival rate (± 1 SE) of adult female (n= 485) and male (n= 849) Green-rumped Parrotlets (*Forpus passerinus*). Nonbreeders (NB) were individuals that did not have a nest cavity but were present on the study site, and breeders (B) were individuals that initiated a clutch. Data from Sandercocock et al. 2000.**

Johnston *et al.* (1997) estimated the annual survival of tropical forest passerines in a long-term mist-netting study in Trinidad to be 65% (n= 17 species). They used analytical models to remove any bias caused by young and transient birds in their sample. Even then, they suggest they have likely underestimated survival. Faaborg and Arendt (1995) found a survival rate of 68% using capture-recapture data for 9 Puerto Rican passerines. Johnston *et al.* (1997) used a linear contrast comparative method to control for phylogenetic effects, and found that tropical species have a significantly higher annual survival rate than comparable temperate zone birds.

No matter which method of survival estimation is used (long-term monitoring of individuals versus capture-recapture), tropical birds average higher survival than comparable temperate zone birds.
A powerful test is to compare survival in a genus that occurs in both temperate and tropical regions (unlike manakins, antbirds and Hawaiian honeycreepers). Ricklefs (1997) used museum collections to estimate survival of New World *Turdus* thrushes to be higher in tropical (0.76–0.85) than north temperate (0.56) species.