

Extended parental care and delayed dispersal: northern, tropical, and southern passerines compared

Eleanor M. Russell,^a Yoram Yom-Tov,^b and Eli Geffen^c

^a53 Swan Street, Guildford, Western Australia 6055, Australia, ^bDepartment of Zoology, Tel Aviv University, Tel Aviv 69978, Israel, and ^cInstitute of Nature Conservation Research, Tel Aviv University, Tel Aviv 69978, Israel

Using modern comparative methods, we found that both time to independence and time with parents were significantly longer in southern hemisphere and tropical birds than in northern hemisphere ones. These differences held even after removing Australian passerines or cooperatively breeding species, and they do not depend on habitat, diet, or migration pattern. In southern hemisphere and tropical regions, both cooperative breeding and non-cooperative parents continue to feed their young for a similar length of time, but cooperative breeders allow them to stay longer in their natal territory after they become nutritionally independent. Nevertheless, the young of non-cooperative species stay longer with their parents than do the young of non-cooperative species in the temperate northern hemisphere. The fact that extended periods of post-fledging parental care are widespread among passerines provides further empirical support for the view that life histories of southern and tropical birds are 'slow,' with small clutches, extended parental care, and long lifespan; parents take care of fewer young for longer. These results support recent theoretical models that predict that high adult survival and low turnover of territory owners generally favor natal philopatry. We suggest that the reasons why some species (with or without cooperative breeding) exhibit natal philopatry and others do not lie in the balance between productivity and survival of adults and of retained or dispersing offspring. *Key words:* Life history, delayed dispersal, parental care. [*Behav Ecol* 15:831–838 (2004)]

Variation in life history parameters may enhance the understanding of ecology and phylogeny of animals. Birds of the tropics and temperate southern hemisphere show consistent differences in their life histories when compared to their temperate northern hemisphere counterparts, and these differences have attracted much attention from zoologists. A review by Martin (1996) summarized the general view that birds of the tropics have smaller clutches (Klomp, 1970; Lack, 1947; Moreau, 1944; Murray, 1985; Yom-Tov et al., 1994), have longer incubation and fledging periods (Lack, 1968; Ricklefs, 1968; Skutch, 1949; but see Geffen and Yom-Tov, 2000), lay more clutches per year (Lack and Moreau, 1965; Ricklefs, 1969a), have longer post-fledging periods (Cody, 1966; Ricklefs, 1973; Skutch, 1985), and have higher survival rates (Faaborg and Arendt, 1995; Fogden, 1972; Snow and Lill, 1974). Many of these life-history attributes are also found in birds of the temperate southern hemisphere (Yom-Tov 1987; Rowley and Russell, 1991). Martin (1996) discussed the conflicting hypotheses of food limitation and nest predation that have been invoked to explain life history variation: reduced seasonality in the availability of food, higher ambient temperatures in the tropics and the southern hemisphere with the lack of a severe winter, and the high proportion of predators (particularly reptiles) in these regions have been related to the differences in life history parameters (Ashmole, 1963; Martin et al., 2000; Rowley and Russell, 1991; Skutch, 1985). It has been argued that the relatively stable environments of the tropics and southern hemisphere result in stable populations and saturated habitat, which in turn favor

a strategy of slow breeding (Rowley and Russell, 1991, Russell, 1989; Russell and Rowley, 2000). In addition to ecology, phylogeny may also influence life history parameters. For example, the old endemics among Australian passerines (mostly Corvida) have small clutches, and this character may be related to their phylogeny rather than to their ecology (Yom-Tov, 1987). Thus, the high proportion of Corvida among the Australian avifauna contributed to the impression that small clutches are common in Australia (Cockburn, 1996).

Martin (1996) examined the validity of the above perceptions and concluded that "we know very little of the causes of differences between north temperate and tropical-southern hemisphere regions, and much of what we think we know about the differences may be incorrect or overstated." One of his conclusions was that in compensation for smaller clutches, parental care may be increased, enhancing the survival of young, who may stay in their parents' territories for extended periods after fledging, but only a few studies were available to support this hypothesis (Fogden, 1972; Skutch, 1976; Willis, 1967, 1972).

Subsequent work tested some of the above perceptions. Geffen and Yom-Tov (2000) used a large database and confirmed that clutch size differs significantly between the tropics-southern hemisphere and the north temperate region, but the length of incubation and fledging periods do not differ between them. However, Martin (2002) showed that the incubation periods of some Argentine passerines are longer than those of their counterparts in Arizona and found that longer incubation periods and smaller clutches were associated with lower adult mortality. He suggested that a focus on age-specific mortality as a major source of selection might provide some insights on life-history evolution. Johnson et al. (1997) confirmed that adult survival is higher in the tropics than in north temperate regions of North America and Europe, and Peach et al. (2001) demonstrated that the

Address correspondence to E. M. Russell. E-mail: icrowley@ozemail.com.au.

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survival of insectivores and nectarivores of southern Africa was higher than that of related European species. Russell (2000) showed that species of the northern hemisphere have patterns in which young associate with their parents for only a short time before having to fend for themselves, while tropical-southern hemisphere birds stay much longer with their parents. However, Russell (2000) did not control for phylogeny, a factor that may strongly influence the outcome of the analysis.

The claim that southern hemisphere and tropical birds have higher re-nesting rates and more broods per year was not strongly supported by Martin's review (1996). To our knowledge, this perception has not been tested on a large sample or by using phylogenetically controlled methods. While high levels of nest predation may result in high re-nesting rates (Brosset and Erard, 1986; Skutch, 1985; Willis, 1974), the production of multiple broods is less clearly supported, with evidence of only one brood per year in many species (Dittami and Gwinner, 1985; Robinson et al., 2000).

Thus, of the five life history parameters listed by Martin (1996) that were perceived to differ between southern hemisphere and tropical birds, on one hand, and northern hemisphere ones on the other, only clutch size and survival have been shown to differ; incubation and fledging periods do not. The number of breeding attempts per year and the length of post-fledging parental care have not been tested by methods that take phylogeny into consideration.

Another aspect of avian life histories that differs between temperate northern hemisphere and the tropical-southern temperate regions is the level of incidence of cooperative breeding. Cooperatively breeding species are not randomly distributed among avian families or throughout the world, and cooperatively breeding families are over-represented in the Australo-Papuan region as well as in lower latitudes (Arnold and Owens, 1998, 1999; Geffen and Yom-Tov, 2000). Several authors failed to find consistent differences in life history between cooperative and non-cooperative birds (Cockburn 1996; Poiani and Jermiin, 1994; Poiani and Pagel 1997). However, Arnold and Owens (1998) have shown that cooperative breeding is associated with longer survival, smaller clutches, and increased sedentariness. Langen (2000) has shown that the duration of post-fledging parental care is significantly longer in species that regularly breed cooperatively, and this relationship is independent of habitat, latitude, and diet. He also showed that adult survivorship and the duration of feeding of fledglings are positively associated. By prolonging brood care, parents may increase the survivorship of their offspring (Verhulst et al., 1997; Weathers and Sullivan, 1989). The occurrence of many cooperative breeders with long periods of post-fledging parental care and long survival may give the impression that these phenomena are typical of all tropical and southern hemisphere birds, but this is not yet reliably established.

Several recent theoretical papers have modeled dispersal and offspring retention in saturated habitats in an attempt to explain the evolution of cooperative breeding (Kokko and Ekman, 2002; Kokko and Lundberg, 2001; Pen and Weissing, 2000). They examine the relative fitness gains for a young bird of staying on a territory versus searching for other sites where there is a limited supply of breeding vacancies. These models agree that high survival of adults promotes delayed dispersal of offspring. Kokko and Ekman (2002) take the view that delayed dispersal requires an explanation that is independent of the evolution of helping, and they cited a small number of species having delayed dispersal in the absence of cooperative breeding.

The aim of this study is to examine the hypothesis that periods of post-fledging parental care are longer in tropical

and southern hemisphere passerines than in those of the temperate northern hemisphere. Specifically, we used modern phylogenetically controlled methods to compare two aspects of post-fledging parental care, namely time to independence and the length of time juveniles were allowed to stay in the family group or territory after fledging. We expected that post-fledging associations with parents would be longer in tropical and southern hemisphere birds than in those of the temperate northern hemisphere. We expected that this would hold not only for cooperatively breeding species but also for non-cooperative species.

MATERIALS AND METHODS

Data

We searched for records of what happens to young birds after they fledge, a stage where many studies cease. We restricted our search to the order Passeriformes, in which young are altricial and require feeding by adults. We searched the ornithological journals *Auk*, *Condor*, *Wilson Bulletin*, *Emu*, *Ibis*, *Notornis*, and *Ostrich* from 1960 to the present, and we also followed any useful leads they suggested. We also searched the books by Brosset and Erard (1986), Chapin (1953, 1954), Maclean (1993), Skutch (1954, 1960, 1967, 1969, 1972, 1981, 1996a,b), Steyn (1996), and van Someren (1956), and the various publications on cooperative breeding by Clarke (1995), Cockburn (1996, 1998), Dow (1980), du Plessis et al. (1995), Grimes (1976a,b), and Rowley (1976). The major continental collections of avian life history information were also searched: *The Birds of Africa* volumes 4–6 (Fry et al., 2000; Keith et al., 1992; Urban et al., 1997), *Birds of the Western Palearctic (BWP)* volumes 5–9 (Cramp 1988, 1992; Cramp and Perrins 1993, 1994a,b), *The Birds of North America* (Poole and Gill 1993–2002), and *The Handbook of Australian, New Zealand, and Antarctic Birds Volumes 5–6* (Higgins and Peter, 2002; Higgins et al., 2001).

We recorded body mass, clutch size, incubation and fledging periods, the nature of post-fledging parental care, and mating system. Body mass (adult male and female) was taken from the original sources, if given, otherwise, it was taken from Dunning (1994). We noted the breeding location, habitat, and diet of each species, as well as its migratory status. For analysis, breeding location was assigned to one of two categories: (1) northern hemisphere temperate regions (NHTE), and (2) tropical and temperate southern hemisphere regions (SHTR). If the species range covered both of these categories, we used the location from which the information was derived. Diet was categorized as (1) primarily animal food or (2) primarily vegetable food (fruit, nectar, seeds). Birds were classified as migrant or resident. Migrant status was applied to long distance migrants and included not only northern hemisphere species flying south from northern Europe to tropical Asia and Africa or from North America to South or Central America, but also some intra-African migrants and species in Australia such as those flying north from Tasmania in winter or south to Australia from Asia and New Guinea. Birds that were altitudinal migrants or local nomads were classified as resident. If a species had both resident and migratory populations, data was used for the predominant state, if possible. Habitat was categorized as (1) closed, in which the upper story of vegetation formed a closed canopy, and (2) open (arid habitats, grassland, shrub steppe, marsh, and savanna woodlands, including the open eucalypt woodlands of Australia).

We recorded three aspects of post-fledging parental care and association:

1. *Time to Independence* (TTI). This is not easy to standardize, because the same term has been used for

different things. Sometimes it is used for the time when fledglings leave or are expelled from the parental territory; at other times, it refers to the time when young are independent of parental feeding. In many north temperate species, these two times are similar and hard to distinguish, and few species accounts in Birds of the Western Palearctic make any distinction. In species that stay for longer, there is a clear distinction between the time when young are independent of parental feeding and the time at which they leave the parental territory, which may be several months later. We measured Time to Independence as the time from fledging to when the young are largely independent of parental feeding. They may still occasionally beg for and receive food from a parent for many months, as in the Australian Magpie *Gymnorhina tibicen*, but they are sustained by their own efforts. Where a range of time was given, the midpoint was used.

2. *Time with Parents* (TWP). This is the length of time that the immatures stay in the parental territory or, in some cases, with their parents but outside the breeding territory. It was the time at which young birds dispersed, and if it was variable or different for males and females, we used the longer time. In some cases, the young, with their parents, joined a flock, and parental care continued in the flock but its duration was impossible to measure; such species were not included in the data analyzed. For many species, only an approximate range of time was available, e.g., 1–3 months, or ‘until the next winter’ or ‘to the next breeding season’. We used the midpoints of ranges and made an approximate estimate of time whenever possible. For species in which immatures were reported as staying until the next breeding season, we estimated 10 months (300 days).
3. *Cooperative breeding*. Many species, northern and southern, live in groups, and of these, some are cooperative breeding, formed by the retention of young in the family group. In some cases it is not definitely known that the helpers in a cooperatively breeding group are the progeny of the breeders, and relationships between group members are unknown. Many species recorded as cooperative breeding are group-living all year round, with sometimes one or two observations of more than two adults feeding at the nest. This includes many of the species listed as possibly cooperative breeding by Grimes (1976a,b) and Dow (1980), and included as cooperative breeding by Brown (1987), Clarke (1995), and Cockburn (1996), who did not distinguish levels of certainty. Because information on cooperatively breeding species is of variable quality, we included data only for species in which, from detailed studies of identifiable individuals, it was definitely known that offspring stayed in their parents’ group for at least one breeding season. Time with Parents was scored as 400 days, approximately to the end of the next breeding season. The many other species listed as cooperative breeding were included in the qualitative analyses of Russell (2000).

The data used in our analyses is available on request from E.M.R.

Statistics

In this analysis we examined the regional change in Time to Independence and Time with Parents of passerines. We examined regional differences between northern hemi-

sphere, southern hemisphere, and tropical birds in each of the variables using *t* tests on log-transformed data. Logarithmic transformation of size data fits the assumption that different lineages are equally likely to go through the same proportional change in scale. In the next step, we removed the effect of body mass prior to testing for regional differences by using residuals from a regression of each of the two variables on body mass. Last, to control for the effect of phylogeny we used the CAIC (comparative analysis by independent contrasts) program (Purvis and Rambaut, 1995) that implements the independent contrasts method (Felsenstein, 1985). The methods implemented in the CAIC program work best when the variables used are continuous or categorical (preferably dichotomous). Polytomies (nodes with more than two daughter branches) that express ignorance of the true branching structure are treated in CAIC according to Pagel (1992). A dendrogram (topologies and branch lengths), based on DNA-DNA hybridizations, provided in Sibley and Ahlquist (1990: 856–869), was used for determining phylogenetic relationships among species. Species not mentioned or specified (represented only as genus) in the Sibley and Ahlquist (1990) dendrogram were treated as sister taxa within their genus. Branch lengths for such species were estimated as mean branch length within the genus (in cases where other species within the genus were indicated) or as the mean branch length within all genera outlined in the dendrogram (in cases where no other species within the genus were indicated). The branch lengths in CAIC are used as a measure of the expected variance that allow standardization of the contrasts. Contrasts between distant species will have higher expected variance (i.e., branch length) than contrasts between sister taxa. Further, simulation studies showed that the independent contrast method is valid even with very inaccurate branch lengths (Martins and Garland, 1991). In light of the relative insensitivity of the contrast method to the distance between taxa, the use of branch length data from Sibley and Ahlquist (1990) is a reasonable measure for the expected variance component between taxons.

For each group of birds we examined the relationship between (1) body mass (independent variable) and two other dependent variables (Time to Independence and Time with Parents) by linear regression, and (2) contrasts of body mass (independent variable) and the contrasts of the other two dependent variables by linear regression through the origin. We performed these initial steps to examine the effect of body mass on other variables before and after the phylogenetic component was removed. All analyses were performed on log-transformed data.

For our regional comparisons we assigned a value of zero to all species in one region and a value of one to all species in the other region, thus creating a categorical character with only two states. Using the Branch option in CAIC, we compared the two dependent variables between regions. The null hypothesis is that evolution in the dependent variable has not been linked to region; thus, we should expect half the contrasts in the dependent variable to be positive and half negative, and the mean value of the contrasts to be zero. We tested the null hypothesis using a *t* test on the mean of the contrasts (Purvis and Rambaut, 1995). A mean significantly greater than zero indicates that in the region assigned as one the values of the dependent variable are larger, whereas a mean significantly below zero indicates larger values of the dependent variable in the region assigned as zero.

RESULTS

At the first stage of the analysis we found that body mass was positively correlated with Time with Parents and Time to

Table 1
Relationship between body mass and the duration of post-fledging parental care in passerines

Character	Raw data						Contrasts					
	Slope	Intercept	<i>r</i>	<i>F</i>	df	<i>p</i>	Slope	<i>r</i>	<i>F</i>	df	<i>p</i>	
Time to independence	0.238	1.03	0.357	48.45	1,332	<.0001	0.210	0.262	17.76	1,241	<.0001	
Time with parents	0.295	1.39	0.254	24.23	1,350	<.0001	0.242	0.172	7.88	1,258	.0054	

Regression coefficients of body mass (independent variable) on two parental care related dependent variables (Time to Independence and Time with Parents). Linear regressions were performed on the raw data (log-transformed) and on the independent contrasts (regression through the origin).

Independence (Table 1). Hence, for all comparisons of life history parameters we also controlled for body mass.

Northern hemisphere versus southern hemisphere and tropics

Contrasts analyses showed that both Time with Parents and Time to Independence were significantly shorter among northern hemisphere passerines than in the southern hemisphere and tropical ones (Table 2).

Australian passerines formed a large proportion (39.2%; $n = 311$) of our southern hemisphere and tropical sample. To test the contribution of Australian birds to the differences between the two large regional samples, we removed Australian species from the comparisons. We found that the significant differences between the northern hemisphere and southern hemisphere remained even after the removal of Australian birds from the SHTR sample.

Cooperative and non-cooperative breeders

Several authors have assumed that young of cooperative breeders stay longer with their parents than do the young of other birds. To test the contribution of cooperative breeders to the differences between the two large regional samples, we removed these birds from the comparisons, and we found that significant differences remained between NHTE and SHTR

birds even after the removal of cooperative breeders from the analysis (Table 2).

Among all birds in our sample, cooperative breeders had significantly longer Time with Parents and Time to Independence than non-cooperative ones (Table 3), and that was the case also for NHTE birds. Time with Parents was also significantly longer in SHTR birds and after removal of the Australian birds from the SHTR sample. However, Time to Independence was not significantly different between cooperative and non-cooperative breeders in the SHTR sample, with or without Australia (Table 3).

Life history parameters

We tested if Time with Parents and Time to Independence are influenced by habitat (closed or open), migration (resident or migrant), or diet (insectivory or vegetarian). We found that habitat had no significant influence on the above life history parameters at any stage of the analysis, whereas migration and diet had such an effect at the two early stages (raw data and contrasts), but these significant effects disappeared when we used contrasts controlled for body mass (Table 4), and the final outcome is that neither diet nor migration had a significant effect on the above life history parameters. These results may indicate that a larger sample could change the outcome of the analysis.

Table 2
Comparison of post-fledging parental care between northern temperate passerines and those of the tropics and southern temperate regions

Character	Raw data			Raw data controlled for body mass			Contrasts				Contrasts controlled for body mass			
	<i>t</i>	df	<i>p</i>	<i>t</i>	df	<i>p</i>	Mean	<i>t</i>	df	<i>p</i>	Mean	<i>t</i>	df	<i>p</i>
All species included														
Time to independence	10.07	351	<.001	9.04	328	<.001	0.066	4.94	39	<.001	0.053	4.30	37	<.001
Time with parents	12.28	364	<.001	11.49	343	<.001	0.122	8.10	41	<.001	0.108	7.10	37	<.001
Australian species excluded														
Time to independence	7.71	274	<.001	6.75	260	<.001	0.062	5.07	36	<.001	0.053	4.52	36	<.001
Time with parents	9.38	279	<.001	8.93	269	<.001	0.121	7.94	38	<.001	0.109	7.57	37	<.001
Cooperative breeders excluded														
Time to independence	9.07	303	<.001	7.54	283	<.001	0.066	4.85	36	<.001	0.053	4.23	34	<.001
Time with parents	11.28	299	<.001	10.47	281	<.001	0.113	8.65	38	<.001	0.099	7.29	34	<.001

Differences (*t* tests) between north temperate (NHTE) and tropical/southern temperate (SHTR) regions in two parental care related variables (Time to Independence and Time with Parents) for all species, excluding the Australian species and cooperative breeders. *t* tests were performed on the raw data (log-transformed), on residuals with body mass, on independent contrasts, and on contrasts controlled for body mass (see text for details). A mean contrast significantly greater than zero indicates that in the SHTR regions the values of the dependent variable are larger, whereas a mean contrast significantly below zero indicates larger values of the dependent variable in NHTE regions.

Table 3
Comparison of post-fledging parental care between cooperatively breeding passerines and those with other social organizations

Character	Raw data			Raw data controlled for body mass			Contrasts				Contrasts controlled for body mass			
	<i>t</i>	df	<i>p</i>	<i>t</i>	df	<i>p</i>	Mean	<i>t</i>	df	<i>p</i>	Mean	<i>t</i>	df	<i>p</i>
All species														
Time to independence	6.14	351	<.001	6.20	330	<.001	0.036	2.82	28	.009	0.035	2.99	27	.006
Time with parents	14.70	370	<.001	15.20	349	<.001	0.142	7.58	31	<.001	0.142	7.68	30	<.001
Tropical and south temperate species														
Time to independence	2.54	173	.012	3.14	158	.002	0.022	1.55	23	.135	0.022	1.54	22	.137
Time with parents	9.88	200	<.001	10.35	186	<.001	0.113	6.43	24	<.001	0.109	6.46	24	<.001
Tropical and south temperate species (Australian species excluded)														
Time to independence	1.64	105	.103	1.36	91	.178	0.023	1.28	12	.226	0.022	0.97	10	.355
Time with parents	4.94	125	<.001	4.27	112	<.001	0.099	4.35	11	.001	0.088	3.47	11	.005
North temperate species														
Time to independence	3.95	172	<.001	2.86	166	.005	0.051	2.79	5	.038	0.055	3.01	5	.030
Time with parents	10.81	160	<.001	10.83	154	<.001	0.188	3.76	5	.009	0.194	4.20	6	.006

Differences (*t* tests) between cooperative breeders and all other social organizations in two parental care related variables (Time to Independence and Time with Parents) for all species, north temperate (NHTE) species, and tropical and southern temperate (SHTR) species. *t* tests were performed on the raw data (log-transformed), on residuals with body mass, on independent contrasts, and on contrasts controlled for body mass. A mean contrast significantly greater than zero indicates that in the cooperative breeders the values of the dependent variable are larger, whereas a mean contrast significantly below zero indicates larger values of the dependent variable in non-cooperative breeders.

DISCUSSION

The main findings of this analysis are that both Time with Parents and Time to Independence were significantly shorter among northern hemisphere passerines than in southern hemisphere and tropical species. This difference holds even after removing Australian passerines or cooperatively breeding species, and it does not depend on habitat, diet, or migration pattern. These results confirm and extend Russell’s (2000) finding that birds inhabiting the tropics and southern hemisphere have long post-fledging parental care and delayed dispersal. Our results support the hypothesis that the small clutches of SHTR birds are balanced by increased parental care that may promote the survival of juveniles (Martin, 1996).

We also found that cooperative breeders had significantly longer Time with Parents and Time to Independence than non-cooperative species, in agreement with Langen’s (2000) conclusion. However, in the southern hemisphere and the tropics Time to Independence is no different between cooperative breeders and non-cooperative species, while Time with Parents was longer in cooperatively breeding species. This means that in the southern hemisphere and the tropics, both cooperative and non-cooperative breeders feed their young for a similar length of time after fledging.

In all species that exhibit delayed dispersal, the young remain with their parents, generally in the parental territory, after they become nutritionally independent. Many young of cooperatively breeding species remain in the parental

Table 4
Effects of habitat, migration and diet on post-fledging parental care in passerines

Character	Raw data			Raw data controlled for body mass			Contrasts				Contrasts controlled for body mass			
	<i>t</i>	df	<i>p</i>	<i>t</i>	df	<i>p</i>	Mean	<i>t</i>	df	<i>p</i>	Mean	<i>t</i>	df	<i>p</i>
Habitat														
Time to independence	1.01	112	.312	1.62	107	.108	-0.008	0.82	25	.418	-0.005	0.49	24	.626
Time with parents	0.40	119	.690	0.55	114	.580	-0.017	0.80	23	.438	-0.008	0.41	22	.684
Migration														
Time to independence	4.65	113	<.001	4.41	108	<.001	-0.021	1.21	14	.245	-0.023	1.47	14	.163
Time with parents	7.79	122	<.001	6.29	117	<.001	-0.062	2.38	12	.035	-0.046	2.06	12	.061
Diet														
Time to independence	3.10	117	.002	2.37	112	.020	0.004	0.18	11	.857	-0.004	0.22	10	.827
Time with parents	3.68	126	<.001	3.58	121	<.001	0.003	0.08	9	.937	-0.004	0.10	9	.919

Differences (*t* tests) in two parental care related variables (Time to Independence and Time with Parents) between open and closed habitats, migratory and resident species, and insect and vegetative feeders. *t* tests were performed on the raw data (log-transformed), on residuals with body mass, on independent contrasts, and on contrasts controlled for body mass (see text for details). A mean contrast significantly greater than zero indicates that species ranked as one (open habitat, migratory, and insectivorous) and the values of the dependent variable are larger, whereas a mean contrast significantly below zero indicates larger values of the dependent variable in species ranked as zero (closed habitat, resident, and vegetative feeders).

territory into the next breeding season, when they help to feed the young of that year. In the majority of cooperatively breeding species, helpers are derived from philopatric young in this way. In many SHTR species that do not breed cooperatively, young birds remain in their natal territory with their parents for up to several months, sometimes until the start of the next breeding season. From data in Table 5 of Russell (2000) and Russell (unpublished data), 105 (31%) of 344 SHTR species with known Time with Parents were cooperative breeders, and in a further 118 (34%), young remained in their natal territory for >100 days, including 57 that remained for >180 days.

These findings, and those of other studies comparing life history traits between the two regions, show that birds inhabiting the tropics and southern hemisphere have adopted a slow breeding strategy; high adult survivorship is associated with small clutches and extended periods of post-fledging parental care (Bennett and Owens, 2002; Martin, 2002; Rowley and Russell, 1991). One aspect of the slow life history that may contribute to the longer periods of parental care is the longer time available for breeding (Wyndham, 1986). A larger proportion of northern species live north of 40° N latitude, compared with the southern hemisphere, where only a relatively small part of South America is south of 40° S latitude. This means that much of the northern avifauna is subject to the longer winters and shorter summers of higher latitudes, which limit the time available for breeding, molting, and accumulating fat reserves either for migration or for the winter. For SHTR species, the time suitable for breeding is longer (Magrath et al., 2000; Woinarski, 1985; Wyndham, 1986), although it is still generally seasonal, even in tropical wet forests (Stutchbury and Morton, 2001; Wikelski et al., 2000).

One reason for the longer Time to Independence may be that breeding attempts are not compressed into the shortest possible time, and breeders have time to feed one brood of fledglings for longer before they turn their efforts to a second brood. Despite some evidence that the inter-brood intervals are longer for SHTR species (Magrath et al., 2000; Ricklefs, 1969b), large-scale comparisons have not been made. However, in many species in which the young stay with their parents long after independence, only one brood is produced. Fogden commented, "...there is no indication that any insectivorous forest species ever attempts a second brood after a successful first, the reason being that there is an extremely prolonged period of parental care...which may last for as long as six or seven months" (1972: 318). For the members of mixed species flocks of insectivores in Neotropical forests, Jullien and Thiollay observed, "no more than one successful reproduction/pair/year has ever been recorded, probably because the young were fed by their parents for an extended period..." (1998: 242). With the high levels of nest predation experienced by antbirds, Willis (1967, 1972, 1973) found that they continued to re-nest until successful and then cared for that young for an extended period. In the song wren *Cyporhinus phaeocephalus* in Panama, although the breeding season was seven months long each year, most pairs were single brooded; once they fledged one brood, they did not start another clutch in that breeding season (Robinson et al., 2000).

Our study and that of Russell (2000) provide empirical evidence that delayed dispersal (including cooperative breeding) is widespread in SHTR passerines, and this is in agreement with the results of several recent theoretical treatments of dispersal (Kokko and Ekman, 2002; Kokko and Lundberg, 2001; Pen and Weissing, 2000). Kokko and Lundberg (2001) investigated how residency strategies (dispersal, migration, philopatry, and delayed dispersal) depend on life history traits and spatial variation in habitat quality. They considered the case of species living in saturated habitat

where there is competition for a limited supply of breeding site vacancies and estimated the relative fitness gains of staying on a territory versus searching for other sites. They showed that competition for breeding sites (habitat saturation) will favor delayed dispersal but is a dynamic outcome of survival rates in resident and dispersing individuals. They take the view that "a 'constraint on independent breeding' in general, and habitat saturation in particular, is not an external property of the environment but arises from birth, death and dispersal in a population occupying a specific area" (Kokko and Lundberg, 2001: 189). The high survival of territory owners in tropical and southern hemisphere regions generally favors natal philopatry, without any need to invoke inclusive fitness benefits from helping. Kokko and Ekman (2002) discuss the special case in which philopatric offspring may inherit their natal territory or shift to a neighboring vacancy, and their results support the idea of the natal territory as a safe haven in which to wait for a breeding opportunity. These models suggest that given delayed dispersal, there is then scope for the evolution of helping behavior.

Cockburn (2003) showed that the occurrence of cooperative breeding is more widespread than generally thought. Of the oscine passerines with biparental care, 19% breed cooperatively. Phylogenetic analysis showed that in most clades with both cooperative and non-cooperative breeding species, the cooperative breeding is unevenly distributed, such that some genera are all cooperative breeding, and others have none. Our work shows that clades that do not exhibit cooperative breeding may exhibit extended parental care and delayed dispersal (e.g., Malaconotini, Vireonidae, Calceatidae, Dasyornithinae, Cinclidae, Estrildinae) and also that in non-cooperative genera in mixed clades that contain both cooperative and pair breeders, extended parental care may occur. In the Troglodytinae (New World Wrens), two genera, *Donacobius* and *Campylorhynchus*, are cooperative breeding; the eight remaining genera for which there are data breed as pairs, but at least in *Thryothorus* and *Cyporhinus*, delayed dispersal is known (Ahumada, 2001; Cockburn, 2003; Robinson et al., 2000; Skutch, 1954, 1976).

Cooperative breeding is part of a slow breeding strategy that enables young to stay longer with their parents, and it has been viewed as an adaptation to environments where the opportunities to establish new breeding territories are rare (Brown, 1987; Emlen, 1982; Rowley and Russell, 1991; Russell 1989). The relatively non-seasonal and stable environmental conditions in much of the tropics and the southern hemisphere may result in stable populations that also favor a slow breeding strategy and cooperative breeding (Bennett and Owens, 2001). At first sight, non-cooperative species with extended parental care share with cooperative species the same life history attributes that are said to favor cooperative breeding—sedentariness, high adult survival, smaller clutches, low latitudes, and a constant environment in terms of temperature variation. This supports Kokko and Ekman's view (2002) that cooperative breeding requires an explanation that is independent of the evolution of delayed dispersal. However, in addition to that, we require an explanation of why some SHTR species have extended parental care and some have not.

Our analyses and those of Langen (2000), Arnold and Owens (1998), and Bennett and Owens (2002) have found no overall effect of diet, migration, and habitat on the occurrence of either cooperative breeding or delayed dispersal. However, these analyses oversimplify the complexity of these factors by reducing each to a small number of categories, e.g., animal or vegetable food. The difference between the wet tropics, with their natural forest cover, and the tropical savannas of Africa, Australia, and South America

is considerable, but as yet the effect of intra-tropical variation on life histories has not been explored, due to lack of information. Even the wet tropical habitats may be seasonal, with considerable variation in insect food availability (Fogden, 1972). SHTR species cannot be treated as a homogeneous assemblage, as shown for passerines of southern Africa; granivores laid larger clutches and lived relatively shorter lives than did insectivores or nectarivores, and Peach et al. (2001) suggested that this may be influenced by the effects of variable and unpredictable rainfall on seed availability. The variability in the timing and amount of rainfall may be significant for many species, especially as so much of the SHTR region is affected by El Niño events.

Martin (2002) demonstrated the importance of adult mortality in explaining geographical patterns of life history variation, specifically in incubation periods and clutch size, and suggests it is an important influence on all aspects of life history and parental care strategies among birds. It is likely that the explanation of why some species have extended parental care and delayed dispersal and some have not lies in the balance between productivity, the survival of adults and offspring (both retained and dispersing), and the resulting level of competition for vacancies, as suggested by the models of Kokko and Lundberg (2001). This balance may be determined by the characteristics of the particular habitat in which the species lives and of its way of life and diet. Comparisons of dispersal patterns and life history between related species will be necessary to explore this further.

This study leaves only one of the five life history parameters perceived to differ between the two regions that has not yet been examined: the number of breeding attempts per year. So far, lack of data from birds of the tropics and southern hemisphere has prevented such an examination, which is timely and will enable a better understanding of the differences in life history of birds between the two regions.

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