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Avian Life Histories: Is Extended Parental Care the Southern Secret?

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Summary: Most theories of life history evolution have been based on demographic studies from cool temperate regions of the northern hemisphere, where many birds either migrate to avoid severe winters or suffer high mortality if they stay. Life histories of species living in tropical and southern temperate regions are typified by smaller clutches, multiple nesting attempts, high levels of nest predation, and high adult survival. Hypotheses explaining the evolution of these different patterns invoke differences in food availability, nest predation or mortality. The difficulty in deciding between different hypotheses lies in the lack of information about the breeding biology of species living in the southern hemisphere. One aspect of life history variation that has received little attention is the survival of juveniles, which requires intensive study of known individuals, difficult in all but sedentary species. Extended parental care may promote

the survival of juveniles, and thus counteract the effects of smaller clutches. I concentrated on the Passeriformes and reviewed the Time to Independence and the length of time for which juveniles were allowed to stay in the family group or territory after fledging. Species of the northern temperate regions show patterns in which young associate with their parents for only a short time before having to fend for themselves, less than one month in a majority of species. This contrasts with patterns of parental care in species of the tropics and southern temperate regions, in which Time to Independence is generally at least one month, and a majority of species remained with their parents for at least three months. I suggest that by increased investment in a few young, total reproductive effort is reduced, which may contribute to higher adult survival. The need for management to take account of life history attributes is emphasised.

The study of avian life histories brings together behaviour, ecology, phylogeny, evolution and population biology. It has its basis in natural history, for it is the different ways birds live that lead us to attempt to explain the significance of these different patterns and how they arose. The life history theory that results needs to be tested against the real world of empirical studies.

The perception is widespread that tropical and southern temperate birds differ from north temperate ones in several aspects of their life histories: laying smaller clutches, laying more clutches per year, longer developmental periods and extended parental care leading to high juvenile survival, and higher adult survival, (see reviews by Skutch 1985; Martin 1996; Ricklefs 2000a,b; also Fogden 1972). Martin (1996) set out to test the validity of these perceptions, using mainly data for the neotropics. He reviewed the major classes of hypotheses advanced to explain differences in life history traits between tropical-southern hemisphere and northern temperate birds — nest predation, food limitation and adult survival. He concluded that ‘we know very little of causes of differences between north temperate and tropical-southern hemisphere regions, and much of what we think we know about differences may be incorrect or overstated’. One of his conclusions was

that to compensate for smaller clutches, parental care may be increased, enhancing the survival of young, for example by allowing them to remain on their natal territories for extended periods after fledging.

Subsequent work has confirmed that adult survival is higher in the tropics than in north temperate regions of North America and Europe (Johnson et al. 1997). Developmental periods are probably no different, with little or no difference between tropical and temperate areas in either incubation or fledging periods, for a large sample of birds; smaller clutches and extended post fledging periods, necessary for juvenile survival, were the most significant differences between tropical and north temperate birds (Geffen & Yom-Tov 2000). A recent study by Martin et al. (2000) cast doubt on higher nest predation or food limitation as being responsible for life history differences between northern and southern or tropical birds, and lends support to the view that small southern clutches result from reduced adult mortality, favouring reduced reproductive effort and/or allocation of greater investment in fewer young.

Although extended parental care leading to higher juvenile survival has been suggested as an important aspect of life histories, little evidence has been assembled to support this proposal; two authors are quoted as

the main sources of information. In his study of forest birds in Sarawak, Fogden (1972) recorded many passerine species in which the young birds associated with and were fed by their parents for a long time after leaving the nest. He commented that 'It presumably means that on balance, parent birds which continue to feed their first brood substantially increase their chances of survival.' Skutch has more than once noted that 'in warm regions, parents continue to attend their young much longer than in cold northern lands' (Skutch 1981; Skutch 1996b), but in his 1996 book 'Parent Birds and their Young', he provides only a few examples. It is not clear from these authors how widespread the phenomenon is, between families, habitats and continents, and it is this that I have attempted to document by a search through the literature for reports of post-fledging parental care; I found many different patterns. That data is the basis for the rest of this paper, where I use it to investigate two questions: is parental care prolonged in southern and tropical birds, and if so, does it lead to increased survival of juveniles in their first year?

The nature of post-fledging parental care

The data

I searched for records of what happens to young birds after they fledge, and unfortunately found it to be a stage where most studies cease. To reduce phylogenetic variation, I restricted my search to the Order Passeriformes. Data were gathered for 540 species from tropical and temperate regions of Africa, Australia, New Zealand and South America, India and south-east Asia. I searched the ornithological journals *Auk*, *Condor*, *Emu*, *Ibis*, *Notornis* and *Ostrich* from 1960 to the present and followed any useful leads they suggested. I also searched the various books by Skutch (1954, 1960, 1967, 1969, 1972, 1996a,b), Maclean (1993), Brosset & Erard (1986), Chapin (1952, 1953), Steyn (1996), van Someren (1956), 'The Birds of Africa, Vol. 4' (Keith, Urban & Fry 1992), 'The Birds of Africa, Vol. 5' (Urban, Fry & Stuart 1997) and the various publications on cooperative breeding by Grimes (1976a,b), Rowley (1976), Dow (1980), du Plessis et al. (1995), Clarke (1995) and Cockburn (1996, 1998). For comparison, I collected data for a sample of 155 northern temperate species, from *Birds of the Western Palearctic Vol. 5-9* (BWP); Cramp 1988, 1992; Cramp & Perrins 1993, 1994a,b) and the ornithological journals.

In each case, I recorded (if possible) body mass,

clutch size, incubation and fledging periods, the nature of post-fledging parental care, mating system, habitat, diet, whether migrant or resident, breeding success, juvenile and adult survival. Body mass was taken from the original sources if given, otherwise from Dunning (1994). Locations were recorded as: Old World Tropical and Southern Temperate (Africa, India, South-east Asia; OWT); Australasia, Tropical and Temperate (Australia, New Guinea and New Zealand; AUS); Central and South America, Tropical and Temperate (CSAM); North American Temperate (NAM); Western Palearctic Temperate (WP). In general comparisons, NHTE refers to Northern Hemisphere Temperate regions and SHTR refers to Southern Hemisphere and Tropical regions.

Family names used in tables are those used in the *Directory of Australian Birds* (Schodde & Mason 1999), which follows the Sibley & Ahlquist (1990) phylogeny so far as 'what is related to what' but differs in the level of relationship, and distinguishes many more families within the Corvida.

I looked for two things:

(1) *Time to Independence* or the length of post-fledging parental care. This is not easy to standardise, since the same term can be used for different things. Sometimes it may mean 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 north temperate species, these two times are often similar and hard to distinguish, and few species accounts in BWP make any distinction. In species which 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. I took Time to Independence as the time when the young are largely independent of parental feeding. They may still 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 quantitative estimates were available, I have grouped these into four categories of < 20 days, 20-< 40 days, 40-< 60 days, and > 60 days.

(2) *Time with Parents*; 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 different for males and females, I 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. These species were scored separately under the heading of 'Groups and Flocks'. 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'. I used the midpoints of ranges, and made an approximate estimate of time whenever possible. I grouped Time with Parents into five categories: < 30 days, 30 to < 100 days, 100 to < 200 days, 200 to < 300 days, and > 300 days. For species in which immatures were reported as staying until the next breeding season, I estimated ten months (300 days). Many species, northern and southern, live in groups, and of these, some are cooperative breeding. Many of these groups are formed by the retention of young in the family group. In these species, time with the parents was set at 400 days, allowing for at least one breeding season as a group member.

Patterns of parental care

The post-fledging care of offspring by the parents in passerine birds takes many forms, and its duration varies greatly between species. Nestlings generally leave the nest before they are fully grown, and for some days, they are quite helpless and remain cryptic, hidden away until an adult approaches with food, when they beg vociferously. This period may be only 1-2 days or more than a week, until they begin to follow their parents and begin to learn what is food and what is not. In many cases, especially those species with larger broods, broods are divided with each adult caring for some of the fledglings. The division may be stable, with each parent always caring for the same young. Brood division enhances the foraging efficiency of the parents (Anthonisen et al. 1997), and by dispersing the young spatially, it may also reduce the chances of predation. First, I outline the many forms that post-fledging parental care may take:

(1) The young birds leave (disperse) or are expelled from their natal territory as soon as they are independent or shortly thereafter; the parents may then renest or prepare to migrate. The young take their chance on their own, feeding in habitat not occupied by breeding birds. They may exist in the gaps between, or in the margins of, territories until they migrate or find a territory for themselves. In species that lay a second clutch, the timing of the expulsion of the first brood may be determined by the hatching of the second clutch. In this case, the male and female together feed their first brood

of fledglings for a few days, then the female begins a second clutch, leaving the care of the fledglings to the male. When the second clutch hatches, the male deserts the first brood and turns his attention to the second. The first brood of fledglings are either chased away or drift away of their own accord. It is not uncommon for young of the second brood to be tolerated longer than those of the first.

Examples: NAM, Northern Mockingbird *Mimus polyglottos* (Zais & Breitwisch 1989); WP, European Robin *Erithacus rubecula* (Harper 1985); Sedge Warbler *Acrocephalus schoenobaenus* (Cramp 1992); warblers of the genus *Sylvia*; CSAM, Large Cactus Finch *Geospiza conirostris* (Grant & Grant 1989); AUS, Willie Wagtail *Rhipidura leucophrys* (McFarland 1984).

(2) As soon as the young are able to fly well, the parents and young leave the breeding territory or nesting area (in colonial breeders) and join a flock. The parents continue to feed the young in this flock, but are very hard to observe, and eventually the juveniles become independent members of the flock. These flocks may be small, just a few local breeding pairs and their young, or they may number thousands.

Examples: WP, Sparrows *Passer* spp. (Summers-Smith 1988); OWT, Finches *Spermestes* spp., *Sporaeoginthus* spp. (Maclean 1993); AUS, Finches *Poephila* spp. and *Taenopygia guttata* (Immelmann 1965; Zann 1976, 1994); Little Raven *Corvus mellori* (Rowley 1973); NAM, Blackbirds *Agelaius* spp. (1996c); CSAM, Caciques and Oropendolas *Cacicus* spp., *Psari-colius* spp. (Skutch 1996b).

(3) Young birds disperse as soon as they are independent and join another adult pair or establish a territory for themselves by the autumn. This is seen in several northern hemisphere resident species such as tits and nuthatches. In the Marsh Tit *Parus palustris* (Nilsson & Smith 1989) and Willow Tit *P. montanus* (Ekman 1989), the young birds stay with their new group during the winter and may fill a breeding vacancy if an adult dies, or move to another group. Young European Nuthatches *Sitta europaea* (Matthysen 1987) may establish a territory by July or August but if no vacancy is found they may associate with a pair in a territory, or float over several territories.

(4) The parents leave the breeding territory when their young are capable of flight and wander as a family either until they migrate, as in the Yellow Wagtail *Motacilla flava* (WP; Smith 1950), or throughout the non-breeding season, as in the Common Amakihi of Hawaii, *Viridonia virens* (van Riper 1987).

(5) Young birds disperse and join a juvenile flock. This may occur as soon as the young are independent, as in the Tree Sparrow *Passer montanus* (WP; Summers-Smith 1988), Chaffinch *Fringilla coelebs* (WP; Newton 1972), Greenfinch *Carduelis chloris* (WP; Newton 1972), Yellow-eyed Junco *Junco phaeotus* (NAM; Sullivan 1989) or some time later, as in the Australian Raven *Corvus coronoides* (Rowley 1973).

(6) Young join (are taken to) a creche — a 'static juvenile flock', differing from other flocks in that some adults are associated with it. The parents of young birds in the creche visit it to feed their young. After leaving the creche, young birds may join the flock or group as in the Pinyon Jay *Gymnorhinus cyanocephalus* (Marzluff & Balda 1992) and the Tricoloured Blackbird *Agelaius tricolor* of North America (Skutch 1996b), or remain in their parents' home range as in the New Zealand Stitchbird *Notiomystis cincta*. (I. Castro pers. comm.).

(7) Young birds may stay in the parental territory beyond independence, often until they moult into adult plumage or after, sometimes even while their parents rear a second brood.

Examples: CSAM, Long-winged Antwren *Myrmotherula longipennis* (Jullien & Thiollay 1998), Checker-throated Antwren *M. fulviventris* (Greenberg & Gradwohl 1995), Firewood Gatherer *Annumbicus annumbi* (Mason 1985), Orange-billed Sparrow *Arremon aurantiostris* (Skutch 1954); NAM, Cactus Wren *Campylorhynchus brunneicapillus* (Andersen & Andersen 1973); OWT, Banded Broadbill *Eurylaimus javanicus* (Fogden 1972), Yellow-throated Longclaw *Macronyx croceus* (Keith, Urban & Fry 1992); AUS, Western Bristlebird *Dasyornis longirostris* (Smith 1987), Southern Scrub-robin *Drymodes brunneopygia* (Brooker in press), Scarlet Robin *Petroica multicolor* (Robinson 1990), Magpie-lark *Grallina hypoleuca* (Hall 1999).

(8) Young birds may stay until parental territorial behaviour becomes more intense at the start of the next breeding season, when they disperse/are expelled.

Examples: OWT, Cape Batis *Batis capensis* (Broekhuysen 1958), Chinspot Batis *Batis molitor* (Urban, Fry & Stuart 1997), Puffback *Dryoscopus cubla* (Maclean 1993), Grey-headed Bush-shrike *Malacotus blanchardi* (Maclean 1993), Brown-throated Wattle-eye *Platysteira cyanea* (Brosset & Erard 1986), Black-and-white Flycatcher *Bias musicus* (Brosset & Erard 1986), Buff-throated Apalis *Apalis rufogularis* (Brosset & Erard 1986); AUS, Brown Thornbill

Acanthiza pusilla (Green & Cockburn 1999), Superb Lyrebird *Menura novaehollandiae* (Lill 1986).

(9) Young birds may stay through the next breeding season until the new young fledge, when the previous year's young are forced to leave.

Examples: NAM, Grey Jay *Perisoreus canadensis* (Strickland & Ouellet 1993); CSAM, Green Jay *Cyanocorax yncas* (Gayou 1986).

(10) Young birds are allowed to stay through the next breeding season and beyond. They do not feed young, but help in territory defence. Examples: WP, Arctic Jay *Perisoreus infaustus* (Ekman et al. 1999). In the African Ruppell's Long-tailed Starling *Lamprolornis purpuropterus*, the young stay in the parental territory, but retreat to the edge of the territory while the parents are nesting (Dittami 1987).

(11) Some young may stay for one or more years and help in feeding young, defending the territory, and generally participating in group life. This is the situation generally called Cooperative Breeding. Some stay for just one breeding season, others for very much longer.

Examples: WP, Arabian babbler *Turdoides squamiceps* (Zahavi 1990); OWT, Chestnut-bellied Starling *Spreo pulcher* (Wilkinson 1982), Jungle Babbler *Turdoides striatus*, (Gaston 1978a), Chestnut Wattle-eye *Platysteira castanea* (Brosset & Erard 1986), Chestnut-fronted Helmet-shrike *Prionops scopifrons* (Maclean 1993); CSAM, Bicoloured Wren *Campylorhynchus griseus* (Austad & Rabenold 1985), Stripe-backed Wren *C. nuchalis* (Rabenold 1990), White-throated Magpie-jay *Calocitta formosa* (Langen & Vehrenkamp 1999); NAM, Mexican Jay *Aphelocoma ultramarina*, Florida Scrub Jay *A. coerulescens* (Woelfenden & Fitzpatrick 1984); AUS, Fairy-wrens of the genus *Malurus*, (Rowley & Russell 1997), Black-faced Woodswallow *Artamus cinereus* (Rowley 1999), White-winged Chough *Corcorax melanorhamphos* (Rowley 1978), Grey-crowned Babbler *Pomatostomus temporalis* (Cale 1999).

In categories 8-11, it must be stressed that not all young birds stay; some, especially females, may disperse after a few months.

Because information on whether a species is cooperative breeding is of variable quality, I distinguished cooperative breeding and group living species at 4 levels:

(1) Species in which, from detailed studies of banded birds, it was definitely known that offspring stayed in their parent's group for at least one breeding

season. Time with Parents was scored as 400 days, approximately to the end of the next breeding season. (CB)

(2) Species definitely known to be cooperative breeding, from many observations showing that more than two adults fed at the nest or fed the young, but where it is not definitely known that the helpers are the progeny of the breeders, and relationships between group members are unknown. (CBUNKREL)

(3) Species that 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. This category also includes species in which the only 'helping' observed was by young of the first brood, seen to feed second brood nestlings (e.g. *Cinclosoma castanea* Chestnut Quail-thrush, Brooker 1969). (POSSCB).

(4) Because so many species in Africa, South America and Australia were recorded as occurring in groups or as family parties, even if no detail of time spent with the parents was available, I assigned these species to a category 'family groups'.

Do southern and tropical parents look after their young for longer?

I have used histograms to compare aspects of parental care between passerines of the tropics and the three southern continents (SHTR) with those of northern temperate regions (NHTE). This is the first stage of a test of the hypothesis that southern and tropical species with low reproductive rates invest more in the care of young after they fledge. Some families, especially those with a high incidence of cooperative breeding, are over-represented. For others, there is very little information, especially on the birds of South America. Because of the uneven nature of the information, I have not presented analysis of the quantitative data in this paper, but have used the larger data set which includes estimates of the nature of post-fledging parental care, even if the duration is not exactly known. For this reason, I have not made allowance for phylogeny, and the presence of groups of related species by using methods incorporating Independent Contrasts (Felsenstein 1985).

Time to Independence

I located information on the Time to Independence for 347 species, 126 NHTE and 220 SHTR. Comparison of Time to Independence for NHTE and SHTR species (Fig. 1) shows that the two distributions are very different ($\chi^2 = 76.0$, $d.f. = 3$, $P < 0.001$), with many more periods greater than 40 days in the SHTR species and only 18% of periods less than 20 days, compared with NHTE species, for which 60% were independent in < 20 days. The median Time to Independence for SHTR species is 31.5 days (range 7-200), significantly longer than the median of 15.5 days for NHTE species (range 5-90 days, Mann-Whitney U -test, $z = 9.44$, $n_1 = 222$, $n_2 = 126$, $P < 0.001$), with a much broader scatter of the times, especially above the median, with some very long ones. Although these measures of Time to Independence are correlated with body mass, the correlation is weak ($r = 0.32$, $P < 0.001$, $n = 341$), and explains less than 10% of the variation; it is influenced by the particularly long Times to Independence of some of the larger birds. NHTE and SHTR species do not differ in the proportion of larger birds ($\chi^2 = 2.74$, $d.f. = 3$, $n = 645$, $P = 0.43$) or in median mass (SHTR 27.0 g, range 5-900; NHTE, 24.0 g, range 5.3-561 g, Mann-Whitney U -test, $z = -0.18$, $P = 0.857$, $n_1 = 491$, $n_2 = 154$).

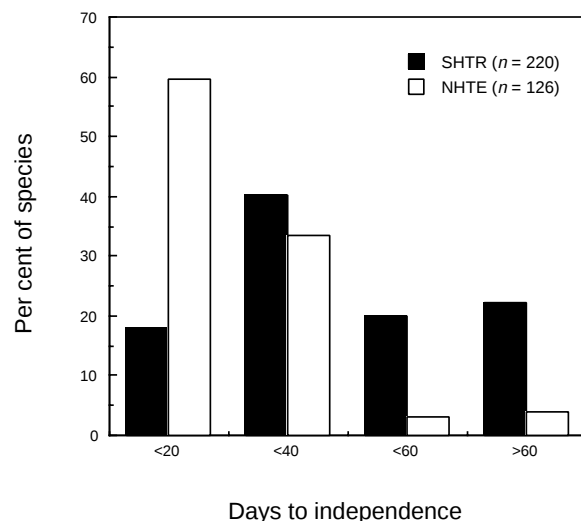


Figure 1 Comparison of the Time to Independence between species of northern hemisphere temperate regions (NHTE, $n = 126$) and southern hemisphere and tropical regions (SHTR, $n = 220$). Values are per cent of species in each of the four categories.

Although for many families there was data for only a few species, Tables 1 and 2 show that the tendency for a longer Time to Independence was spread over a wide range of families, especially those in the SHTR regions. Some endemic families, including the Acanthizidae, Artamidae, Furnariidae, Maluridae and Thamnophilidae had no species with Time to Independence less than 20 days; 90 days or longer was found for 21 species, including only one NHTE species, the cooperative breeding Florida Scrub Jay *Aphelocoma coerulescens* (Woolfenden & Fitzpatrick 1984).

Most of the NHTE species with known Time to Independence greater than 40 days are relatively large, resident corvids (Table 3). The NHTE species with the shortest Times to Independence include both migrants (swallows, wagtails and warblers) and residents (tits and sparrows). SHTR species with short Times to Independence (< 20 d) particularly came from the families Sylviidae, Emberizidae, Estrildidae, Nectarinidae and

Table 1 Time to Independence for 126 species from Northern Hemisphere Temperate regions (NHTE). Values are the number of species in each family for which information was located. The number of genera and species is given in parenthesis after each family name.

Family	< 20 d	20-40 d	40-60 d	> 60 d
Aegithalidae (1, 1)	1			
Alaudidae (3, 3)	2	1		
Certhidae (2, 3)	2	1		
Cinclidae (1, 1)	1			
Cisticolidae (1, 1)	1			
Corvidae (9, 14)		7	2	5
Emberizidae (17, 23)	15	8		
Fringillidae (3, 6)	4	2		
Hirundinidae (3, 6)	6			
Laniidae (1, 4)		4		
Motacillidae (2, 4)	3	1		
Muscicapidae (4, 22)	12	10		
Paridae (2, 8)	7	1		
Passeridae (2, 4)	4			
Prunellidae (1, 2)	2			
Regulidae (1, 1)	1			
Sittidae (1, 1)	1			
Sturnidae (3, 3)	2	1		
Sylviidae (7, 18)	13	3	2	
Tyrannidae (1, 1)		1		
Total (65, 126)	77	40	4	5

Table 2 Time to Independence for 220 species from Southern Hemisphere and Tropical regions (SHTR). Values are the number of species in each family for which information was located. The number of genera and species is given in parenthesis after each family name.

Family	< 20 d	20-40 d	40-60 d	> 60 d
Acanthisittidae (1, 1)		1		
Acanthizidae (5, 9)		3	5	1
Alaudidae (2, 2)		2		
Artamidae (4, 4)		2	1	1
Campephagidae (2, 4)	1			3
Certhidae (2, 3)		3		
Cisticolidae (2, 5)	3	2		
Climacteridae (2, 4)	1	2		1
Conopopopagidae (1, 1)			1	
Corcoracidae (1, 1)				1
Corvidae (6, 10)		3	3	4
Dicruridae (8, 11)	3	5		3
Emberizidae (10, 13)	5	3	5	
Estrildidae (4, 6)	4	2		
Eurylaimidae (1, 1)				1
Fringillidae (2, 2)		2		
Furnariidae (4, 6)		6		
Hirundinidae (3, 5)	2	3		
Laniidae (1, 2)			2	
Malaconotidae (5, 9)	1	3	3	2
Maluridae (2, 12)		12		
Meliphagidae (8, 11)	2	6	1	2
Motacillidae (2, 3)		3		
Muscicapidae (15, 19)	1	10	6	2
Nectariniidae (3, 7)	6			1
Neosittidae (1, 1)			1	
Orthonychidae (1, 1)	1			
Pachycephalidae (3, 4)		1	1	2
Paradiseaeidae (3, 4)			2	2
Paridae (1, 1)			1	
Passeridae (1, 1)	1			
Petroicidae (4, 8)	1	6	1	
Ploceidae (7, 7)	4	1	1	1
Pomatostomidae (1, 2)				2
Ptilonorhynchidae (4, 5)			2	3
Pycnonotidae (4, 11)	2	2	2	5
Sturnidae (7, 8)	3	2	2	1
Sylviidae (5, 8)	2	2	1	3
Thamnophilidae (4, 5)		3	1	1
Tyrannidae (2, 2)		1		1
Zosteropidae (1, 1)		1		
Total (145, 220)	43	92	42	43

Table 3 Time to Independence for Northern Temperate (NHTE) and Southern Temperate and Tropical species (SHTR); species shown are selected from the shortest and longest times to independence (TTI) for each region. Abbreviations: R: Resident; M: Migrant; N: Nomad; Afr: Africa; Aus: Australia; CRic: Costa Rica; Eur: Europe; Fr. Gui: French Guiana; Galap: Galapagos Islands; Loc: Location; NG: New Guinea; NZ: New Zealand; NAm: North America; Sar: Sarawak.

Species	Loc	R/M/N	Mass (g)	TTI	Source
NHTE < 20 days					
<i>Hirundo rustica</i> Barn Swallow	Eur	M	17	5.3	Cramp & Simmons 1988
<i>Hirundo daurica</i> Red-rumped Swallow	Eur	M	22	5	Cramp & Simmons 1988
<i>Passer hispaniolensis</i> Willow Sparrow	Eur	R	29	5	Summers-Smith 1988
<i>Motacilla alba</i> White Wagtail	Eur	M	22	5.5	Cramp & Simmons 1988
<i>Parus palustris</i> Marsh Tit	Eur	R	11.9	7	Nilsson 1989
<i>Parus varius</i> Varied Tit	Eur	R	17	7	Higuchi & Momose 1981
<i>Carduelis chloris</i> Greenfinch	Eur	R	30	9	Cramp & Perrins 1994
<i>Hippolais polyglottos</i> Melodious Warbler	Eur	R	10.3	9	Cramp & Simmons 1992
<i>Troglodytes troglodytes</i> European Wren	Eur	R	10	9	Cramp & Simmons 1988
NHTE > 40 days					
<i>Pica pica</i> Black-billed Magpie	Eur	R	234	42	Birkhead 1991
<i>Pica nuttalli</i> Yellow-billed Magpie	NAm	R	165	42	Birkhead 1991
<i>Turdoides squamiceps</i> Arabian Babbler	Israel	R	74	45.5	Zahavi 1990
<i>Corvus caurinus</i> Northwestern Crow	NAm	R	415	77	Caffrey 1992
<i>Corvus brachyrhynchos</i> Western American Crow	NAm	R	458	60	Butler et al. 1984
<i>Aphelocoma coerulescens</i> Florida Scrub Jay	NAm	R	80	90	Woolfenden & Fitzpatrick 1984
SHTR < 20 days					
<i>Quelea quelea</i> Quelea	Afr	N	18	10	Ward 1965
<i>Lalage tricolor</i> White-winged Triller	Aus	M/N	26	10.5	Immelmann 1966
<i>Nectarinia famosa</i> Malachite Sunbird	Afr	R	8.7	11	Wolf & Wolf 1976
<i>Geospiza conirostris</i> Large Cactus Finch	Galap	R	28	14	Downhower 1978
<i>Sporaeginthus subflavus</i> Orange-breasted Waxbill	Afr	R	7.3	14	Colahan 1982
<i>Ephthianura albifrons</i> White-fronted Chat	Aus	N	12	14	Major 1991
<i>Cisticola juncidis</i> Fan-tailed Cisticola	Afr, Asia	R	9.4	15	Urban et al. 1997
<i>Taeniopygia guttata</i> Zebra Finch	Aus	R	13	17.5	Zann 1994
SHTR > 100 days					
<i>Pomatostomus superciliosus</i> White-browed Babbler	Aus	R	40.5	105	Cale 1999
<i>Criniger phaeocephalus</i> Crestless White-throated Bulbul	Sar	R	—	105	Fogden 1972
<i>Alophoixus phaeocephalus</i> Yellow-bellied Bulbul	Sar	R	35	106	Fogden 1972
<i>Paradigalla brevicauda</i> Short-tailed Paradigalla	NG	R	108	108	Frith & Frith 1990
<i>Myrmotherula longipennis</i> Long-winged Antwren	FrGui	R	9	90-180	Jullien & Thiollay 1998
<i>Eurylaimus javanicus</i> Banded Broadbill	Sar	R	24.5	140	Fogden 1972
<i>Stachyris erythrops</i> Red-winged Tree Babbler	Sar	R	13	148	Fogden 1972
<i>Stachyris poliocephala</i> Grey-headed Tree Babbler	Sar	R	24	161	Fogden 1972
<i>Calocitta formosa</i> White-throated Magpie-jay	CRic	R	205	180	Langen & Vehrenkamp 1999
<i>Corcorax melanorhamphos</i> White-winged Cough	Aus	R	372	200	Heinsohn 1991

Ploceidae. While the species with very short Times to Independence are all small, Table 3 shows that long Times to Independence are found in small species such as antwrens, small babblers and bulbuls as well as in large birds such as corvids.

Too little information was available for SHTR species that are migratory or nomadic over large distances to allow comparison between residents and migrants. For resident NHTE species, the median Time to Independence was 19 days (range 5-90, $n = 59$), and for migrants, it was slightly shorter (median 15 days (range 5-35, $n = 68$), but the difference was probably not significant (Mann-Whitney U -test, $z = 1.928$, $P = 0.054$).

No clear pattern relates Time to Independence and diet, but certain tendencies emerge. Many of the species with a short Time to Independence are seed-eaters, finches and finch-like birds of the Emberizidae, Estrilidae, Fringillidae and Ploceidae. In some purely nectar feeding species such as the sunbirds of Africa, *Nectarinia*, young birds are independent of their parents very soon. Young Malachite Sunbirds *N. famosa* can feed on nectar from Aloe flowers four days after leaving the nest, and the Lesser Double-collared Sunbird *N. chalybea* within seven days (Schmidt 1964; Wolf & Wolf 1976). Some insect eating species, such as swallows, become self-supporting quickly and are independent in less than 10 days (Table 2). The breeding season of most NHTE species is in the northern spring-early summer when days are long and food very readily available, particularly the caterpillars etc. that are fed to the nestlings of many species. Among such abundance, it is probably not difficult for young to find enough food for themselves, after a short time. On the other hand, if food is scarcer, or more difficult to find, or requires the learning of special skills to catch, then the Time to Independence may well be longer. For example, the Eastern Kingbird *Tyrannus tyrannus* of North America, a tyrannid flycatcher, is an aerial forager that catches prey by hawking from a perch. It is not independent of parental feeding until 4-5 weeks post-fledging, and Morehouse & Brewer (1968) argue that the skills of aerial foraging take a long time to learn.

Fogden (1972) explained the prolonged parental care that he observed in many forest birds in Sarawak, both insect and fruit eaters, in terms of the difficulties involved with the exploitation of scarce food and the use of highly skilled feeding methods, an explanation first proposed by Ashmole & Tovar (1968). Fogden suggested that in the Sarawak forests, besides the

skilled aerial foragers such as trogons, drongoes and flycatchers, most species searched for food in foliage. This technique sometimes requires great skills in prey detection, because of the great diversity and complexity of protective adaptations in the prey. Fogden argued that the long period of parental care characteristic of many insectivorous species provides the opportunity to learn from parents how to 'see through' complex protective adaptations. A similar argument can be applied to the ant-following species such as the antbirds, antwrens and ant-shrikes of South America studied by Willis (1967, 1972, 1973), Oniki (1975), Greenberg & Gradwohl (1985) and Jullien & Thiollay (1998). The actual catching of ants and insects disturbed by them is not difficult; it is the complex swarming behaviour of the ants that has to be learned. In some species, a long period with the parents, whether as helper or not, may be necessary to perfect a specialised feeding technique, as in the White-winged Chough *Corcorax melanorhamphos* (Heinsohn 1991). Magrath et al. (2000) suggested that it is learning to find food when food is not so common that is important, particularly in many southern temperate habitats where there are not the same peaks and troughs in the abundance of food as in many northern temperate habitats. Under these conditions, it may take young birds longer to become self-supporting.

Time with Parents

I located estimates of the time young birds spent with their parents for 432 species, with records of whether a species lived in flocks or groups (family or cooperative breeding) for another 206 species. (Tables 4 and 5). Cooperative breeding species in which it was definitely known that young remain with their natal group for at least one breeding season were included in the category of > 300 days with parents. The category 'group' includes cooperative breeding groups with unknown relationships, family groups, and species reported as 'generally occurring in groups' (species in categories 2-4 of the cooperative breeding/groups classification).

Comparison of Time with Parents for NHTE and SHTR species (Fig. 2) shows that the two distributions are very different ($\chi^2 = 101.2$, $d.f. = 4$, $P < 0.001$), with only 12% of periods for SHTR species less than 30 days, compared with 60% of NHTE species. The number of cooperative breeding SHTR species is largely responsible for the 30% whose Time with Parents is more than 300 days, but a significant number of species that do not breed cooperatively also fall into this category

(see Table 7). However, 31% of SHTR species have a Time with Parents of 100-300 days, much greater than the 5% of NHTE species. The median Time with Parents for SHTR species is 150 days (range 10-400, $n = 305$), significantly larger than that for 127 NHTE species (median 30 d, range 5-400; Mann-Whitney U -test, $z = 9.18$, $P < 0.001$). For migratory NHTE species, of course, a time of more than three months is unlikely, and for the majority of species, the time is less than 50 days. The longer times are those of the few cooperative breeding species, Old World babblers and New World Jays. On the other hand, the SHTR species show a broad scatter of times, especially above the median. Although the measure of Time with Parents is correlated with body mass, the correlation is very weak ($r = 0.12$, $P < 0.02$), and explains less than 2% of the variation. The two groups of species do not differ in the proportion of larger birds ($\chi^2 = 2.74$, $d.f. = 3$, $P = 0.43$), or in median body mass (SHTR, median body mass 27.0 g, range 5-900 g, $n = 295$, NHTE, median 22.8 g, range 5.3-561 g, $n = 127$; Mann-Whitney U -test, $z = -0.132$, $P = 0.895$).

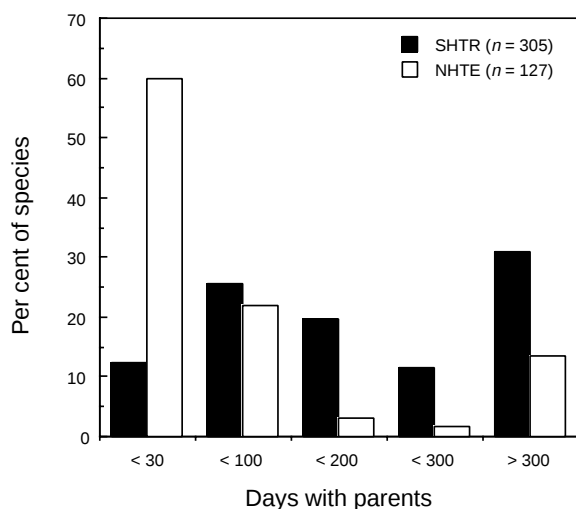


Figure 2 Comparison of the Time spent by independent young, post-fledging, in their parental territory or with the parental group, for species of northern hemisphere temperate regions (NHTE, $n = 127$) and southern hemisphere and tropical regions (SHTR, $n = 305$). Category labels are shortened for convenience, e.g. the category < 300 days includes periods > 200 days and < 300 days. This group includes young reported as staying with their parents until the next breeding season. The category > 300 days includes cooperative breeding species, where young birds stay with their family through the next breeding season and possibly longer.

In the NHTE species sampled, a territorial breeding pair whose young disperse almost as soon as they become independent is the most frequent situation. This is also a common situation in SHTR species, but is surpassed there (when all species surveyed are included) by the total of species that live in cooperative breeding or long-lasting family groups. The high proportion of cooperative breeding species arises in part because parental care and the fate of juveniles is more obvious in such species, and in part because of the large numbers of species of African babblers (Sylviidae, Timaliini) recorded as group-living and probably cooperative breeding. Flocks and juvenile flocks are a significant component in all areas, especially in the Estrildidae, Fringillidae, Emberizidae and Passeridae. Some of the NHTE records of cooperative breeding and group living are for babblers in southern parts of the Western Palaearctic regions and in northern parts of India; the rest are corvids, in particular the New World jays such as *Aphelocoma*, *Cyanocorax*, *Cyanocitta*, *Perisoreus* and *Gymnorhinus*. These figures are based on only a small proportion of all species, and may be biased by unequal sampling of regions and families, but they suggest that a greater proportion of SHTR species has some form of group-living, and young do not leave their parents after only a short time to make their way on their own, but either join some form of social group or remain in their parental group.

Among the species that spend the shortest times with their parents (Table 6) are those which leave their parents and join a juvenile flock, and those whose parents renest rapidly after their first brood fledges and chase their first brood away (e.g. *Ficedula hypoleuca* and *Troglodytes aedon*). Others include species that breed in far northern latitudes, such as *Plectrophenax* and *Calcarius*. Species that spend a short time with their parents include both residents and migrants. The NHTE families in which the young of many species spend 50 days or more with their parents before dispersal are the Corvidae and some Sylviidae (Timaliini, the babblers, some of which occur in temperate regions of the northern hemisphere). Other species which may have long associations with their parents are some of the wheatears of southern Europe and the Middle East and *Baeolophus bicolor* of North America.

For SHTR species, many families have no species whose young spend less than one month with their parents (Table 5). Some of these families are represented by only one species, but of those families represented by more than 10 species, all have a majority of species

with either longer times with parents or with young birds seen in persistent family groups or flocks. Families in which a significant proportion of species spend more than three months on the parental territory or in a cooperative breeding group include the Acanthizidae, Corvidae, Maluridae, Furnariidae, Laniidae, Malaconotidae, Muscicapidae, Pycnonotidae and Thamnophilidae. Among the relatively few SHTR species that spend one month or less with their parents are several seed eaters (*Quelea quelea*, *Geospiza fortis*, *G. conirostris* and *G. scandens*), several nectar feeders (African sunbirds *Nectarinia* spp. and *Promerops cafer*) and among the Australian species, the migrant *Lalage*

tricolor and the nomadic meliphagid honeyeaters such as *Xanthomyza phrygia* and *Conopophila albogularis*. Several species not included in this table spend a short period with parents or mother only, and then the family joins a flock where the family association continues for an unknown time (e.g. Oropendolas *Psarocolius* spp. of South America, many of the *Agelaius* blackbirds of North and South America, some *Lamprotornis* and *Onychognathus* starlings of Africa).

In many species that are not cooperative breeding, progeny are tolerated in the parental territory for several months, in many cases up to the next breeding season. The range of families is shown in Table 5, and

Table 4 Time spent with parents in the parental territory or elsewhere: 146 birds of northern temperate (NHTE) areas. Values are the number of species in each family for which information was located. The number of genera and species is given in parenthesis after each family name. Species for which actual estimates of Time with Parents were not available are included if species could be assigned to the category 'group' or 'flock'. Flock includes juvenile flocks; groups includes known and possible cooperatively breeding species, and species reported as occurring in family groups outside the breeding season. Cooperatively breeding species for which it was known that young birds remained in the group until the next breeding season are included in the column > 300 d.

Family	< 30 d	-100 d	-200 d	-300 d	> 300 d	Groups	Flocks
Aegithalidae (2, 2)			2				
Alaudidae (2, 2)	2						
Bombycillidae (1, 1)		1					
Certhidae (2, 5)	2	1				2	
Cinclidae (1, 1)		1					
Cisticolidae (1, 1)	1						
Corvidae (11, 21)		4	1		11	4	1
Emberizidae (15, 26)	16	3				1	6
Fringillidae (3, 6)	5	1					
Hirundinidae (1, 2)	1			1			
Laniidae (1, 4)	1	3					
Motacillidae (2, 5)	4	1					
Muscicapidae (10, 23)	16	4	2			1	
Paridae (2, 8)	6	1		1			
Passeridae (2, 4)	4						
Prunellidae (1, 2)	1	1					
Regulidae (1, 1)	1						
Sittidae (1, 3)	1				2		
Sturnidae (3, 3)	3						
Sylviidae (10, 25)	14	3			4	4	
Tyrannidae (1, 1)		1					
Total (73, 146)	78	25	5	2	17	12	7

Table 5 Time spent with parents in the parental territory or elsewhere: 492 birds of southern temperate and tropical areas (SHTR). Values are the number of species in each family for which information was located. The number of genera and species is given in parenthesis after each family name. Species for which actual estimates of Time with Parents were not available are included if species could be assigned to the category 'group' or 'flock'. Flock includes juvenile flocks; groups includes known and possible cooperatively breeding species, and species reported as occurring in family groups outside the breeding season. Cooperatively breeding species for which it was known that young birds remained in the group until the next breeding season are included in the column > 300 d.

Family	< 30 d	–100 d	–200 d	–300 d	> 300 d	Groups	Flocks
Acanthisittidae (1, 1)			1				
Acanthizidae (8, 27)	1	4	2	1	5	14	
Alaudidae (1, 1)		1					
Artamidae (4, 10)		1			5	4	
Atrichornithidae (1, 1)		1					
Campephagidae (3, 7)	1	1	1	2		2	
Certhidae (7, 15)		1	3		7	4	
Cinclosomatidae (2, 3)		1	1			1	
Cisticolidae (5, 12)	3	3	1		2	3	
Climacteridae (2, 5)		1			3	1	
Conopopophagidae (1, 1)			1				
Corcoracidae (2, 2)					2		
Corvidae (7, 17)		1	3		5	8	
Dicruridae (7, 11)	1	6		1	2	1	
Emberizidae (27, 47)	11	9	6	2	1	12	6
Estrildidae (6, 8)		5	1				2
Eurylaimidae (1, 1)			1				
Fringillidae (2, 2)		1					1
Furnariidae (8, 9)	1	1	2	2	2	1	
Hirundinidae (3, 4)	1	2		1			
Laniidae (3, 7)			1		2	4	
Malaconotidae (14, 37)		3	7	7	10	10	
Maluridae (5, 26)			3		11	12	
Meliphagidae (13, 28)	5		4	2	3	13	1
Menuridae (1, 1)				1			
Motacillidae (1, 2)		2					
Muscicapidae (14, 25)	2	9	4	3	4	3	
Nectariniidae (4, 10)	5	1				4	
Neosittidae (1, 2)					1	1	
Oriolidae (1, 1)							1
Orthonychidae (1, 1)					1		
Pachycephalidae (4, 9)			2	3		4	
Paradisaeidae (1, 1)			1				
Pardalotidae (1, 1)						1	
Paridae (2, 7)			1		1	5	
Passeridae (1, 1)							1
Petroicidae (6, 12)		6	1		3	2	
Picathartidae (2, 3)						3	
Ploceidae (9, 16)	2		2	2	2	7	1
Pomatostomidae (1, 5)					5		
Ptilonorhynchidae (1, 1)			1				
Pycnonotidae (8, 17)		2	2	1	2	8	2
Sturnidae (10, 21)	2	1		1	9	6	2
Sylviidae (12, 39)	1	2	5	1	1	29	
Thamnophilidae (11, 17)		7	2	3	4	1	
Tyrannidae (10, 13)	1	6	2		1	3	
Vireonidae (1, 1)		1					
Zosteropidae (1, 4)	1					3	
Total (237, 492)	38	79	61	33	94	170	17

Table 6 Time spent in parental territory or with parents for selected Northern Temperate (NHTE) and Tropical and Southern Temperate species (SHTR); species shown are selected from the shortest and longest for each region. No species recorded as regularly cooperative breeding are included. R: Resident; M: Migrant; N: Nomad; TWP Time with Parents. Other abbreviations as Table 3.

Species	Loc.	R or M	Mass (g)	TWP (d)	Reference
NHTE, < 20 days					
<i>Passer hispaniolensis</i> Willow Sparrow	Eur	M	29	5*	Summers-Smith 1988
<i>Hirundo daurica</i> Red-rumped Swallow	Eur	M	22	5	Cramp & Simmons 1988
<i>Carduelis carduelis</i> Goldfinch	Eur	R	16	10	Newton 1972
<i>Ficedula hypoleuca</i> Pied Flycatcher	Eur	M	11.6	10.5	Lundberg & Alatalo 1992
<i>Plectrophenax nivalis</i> Snow Bunting	Eur	N	40	12*	Smith & Marquiss 1995
	NAm	N			
<i>Calcarius pictus</i> Smith's Longspur	NAm	M	29	14	Jehl 1968
<i>Onychognathus tristramii</i> Tristram's Grackle	Israel	R	120	14*	Hofshi et al. 1987
<i>Sturnella magna</i> Eastern Meadowlark	NAm	M	85	14	Skutch 1996b
<i>Parus cinctus</i> Siberian Tit	Eur	R	7	14	Orell et al. 1999
<i>Motacilla alba</i> White Wagtail	Eur	M	22	14	Cramp 1988
<i>Regulus regulus</i> Goldcrest	Eur	R/M	6	14	Cramp 1992
<i>Sitta europaea</i> European Nuthatch	Eur	R	22	14	Matthysen 1987
NHTE, > 60 days					
<i>Garrulus glandarius</i> European Jay	Eur	R	172	60*	Cramp & Perrins 1994
<i>Pica pica</i> Black-billed Magpie	Eur	R	234	60*	Birkhead 1991
<i>Pica nuttalli</i> Yellow-billed Magpie	NAm	R	165	60*	Birkhead 1991
<i>Pyrrhonorax pyrrhonorax</i> Chough	Eur	R	375	60	Cramp & Perrins 1994
<i>Lanius excubitor</i> Great Grey Shrike	Eur	N	66	30-90	Cramp & Perrins 1993
	Asia, N. Afr	R/M			
<i>Oenanthe finschii</i> Finsch's Wheatear	Asia Minor	R	27	> 60*	Cramp 1988
<i>Saxicola dacotiae</i> Canary Island Stonechat	Eur	R	15	> 60	Cramp 1988
<i>Motacilla flava</i> Yellow Wagtail	Eur	R	17	90**	Cramp 1988
<i>Bombycilla garrulus</i> Waxwing	NAm	R	63	30-90*	Cramp 1988
<i>Cyanocitta stelleri</i> Steller's Jay	NAm	R	128	120	Brown 1963
<i>Oenanthe leucura</i> Black Wheatear	S. Eur	R	44	180	Cramp 1988
	NW Afr				
<i>Baeolophus bicolor</i> Tufted Titmouse	NAm	R	22	300	Pravosudova et al. 1999
<i>Corvus corone</i> Carrion Crow	Eur	R	561	365	Coombs 1978
<i>Perisoreus infaustus</i> Arctic Jay	N. Eur, Asia	R	90	> 365	Ekman et al. 1999
SHTR, < 20 days					
<i>Quelea quelea</i> Quelea	Afr	N	18	10	Ward 1965
<i>Lalage tricolor</i> White-winged Triller	Aus	M	26	10.5	Immelmann 1966
<i>Gracula religiosa</i> Indian Hill Mynah	India	R	192	14	Bertram 1970
<i>Nectarinia talatala</i> White-bellied Sunbird	Afr	R	8.2	17.5	Steyn 1966
<i>Prinia maculosa</i> Karoo Prinia	Afr	R	9.1	17-22	Rowan & Broekhuysen 1962
<i>Geospiza fortis</i> Medium Ground Finch	Galap	R	20	14-28	Grant 1986
<i>Promerops cafer</i> Cape Sugarbird	Afr	R	37.5	21	Broekhuysen 1959
<i>Tityra semifasciata</i> Masked Tityra	CSAm	R	88	21	Skutch 1969
<i>Dendrocincla anabatina</i> Tawny-winged Woodcreeper	CSAm	R	40	22	Skutch 1969
<i>Zosterops lateralis</i> Silvereye	Aus	R/M	11	25	Catterall et al. 1989
<i>Xanthomyzon phrygia</i> Regent Honeyeater	Aus	N	43	28	Oliver 1998
<i>Gerygone albofrontata</i> Chatham Island Warbler	NZ	R	9.5	30*	Dennison et. al 1984

* Joins juvenile flock; ** Family joins flock.

Table 7 details all species I located for which estimated time spent in the parental territory was > 200 d (= c. 6 months). This list does not include any known regularly cooperative breeding species and this behaviour is not related to size. *Orthonyx spaldingii* has been recorded as cooperative breeding (Brown 1987; Clarke 1995; Cockburn 1996), but although Jansen (1999) found that it lives in groups, no helpers have been observed (Frith et al. 1996). All species in Table 7 are resident; a few are large species as might be expected (such as *Menura novaehollandiae* and *Orthonyx spaldingii*), but all the others are less than 100 g. Species remaining on the parental territory for a long time have been remarked before by Willis (1973) and three of the species on this list are members of understorey mixed species flocks studied in the forests of French Guiana by Jullien & Thiollay (1998), (*Myrmotherula axillaris*, *M. menestriesii* and *Thamnomanes ardesiacus*). This is clearly not restricted to the Family Thamnophilidae of the forests of South America, but is found in at least 18 families in Central and South America, Africa, Australia, New Zealand and oceanic islands, in both forest and savanna habitats. It is possible that some of these species may be found to be cooperative breeding when studied further, but that is certainly not so for the Thamnophilidae, *Batis* spp., *Orthonyx spaldingii* or *Furnarius rufus*. Many of the species on this list are from African tropical forests and were intensively studied by Brosset & Erard (1986). Whether this way of life is particularly prevalent among African forest species requires similar intensive studies in other habitats and other continents. Table 7 contains very few species from Australia, which may be a real difference or may reflect the lack of information on species from tropical Australia. However, the difference is balanced by the large numbers of Australian species classified as cooperative breeding (either definitely or possibly) in Table 6, and it may be that these are just two different solutions to the same 'problem' of growing up.

Does extended parental care mean increased survival of juveniles?

At the start of this paper, I posed two questions: is parental care prolonged in SHTR species of birds, and if so, does this lead to increased survival of juveniles in their first year? The answer to the first question is obviously that many SHTR birds care for their young for a longer time than NHTE species. Calculations of the survival of juveniles, especially for migratory species, are difficult. Data from large-scale banding requires

sophisticated calculation, and data from small scale individual studies is plagued by dispersal. The data collected provided a good sample of available information for SHTR species, but did not provide a comprehensive list for NH species, which were chosen on the basis of information on post-fledging parental care, not survival. It is an interesting exercise to compare the two groups, but may be of little value in view of the problems caused by dispersal. Nevertheless, the survival of SHTR juveniles was significantly higher than that of NHTE species (SHTR: mean 37.4, $n = 34$; NHTE: mean = 27.6, $n = 22$; $t_{56} = 2.18$, $P = 0.033$).

One might predict that the hazards of migration (for migrant species) and the hazards of severe winters (for residents), coupled with abbreviated parental care, would be reflected in low juvenile survival in the species of northern temperate regions, and this is certainly the case in some species and in some years (e.g. *Junco hyemalis* 10%, *J. phaenotus* 11%, *Parus palustris* 10.1%, *Turdus merula* 11%). For SHTR passerine species, migration, if it occurs, is not long distance across oceans and high mountains, but the hazards of severe winters are replaced by the hazards of droughts, which have effects not only in arid Australia but also in tropical forests and in the large areas of savannas in the Wet-Dry tropics. The unpredictable and severe climatic variation brought about by the El Niño phenomenon and other little-known events in the oceans of the southern hemisphere are likely to be as much of an influence on juvenile survival as are severe winters. But as yet, this is not well documented, apart from the studies of Grant & Grant (1989) in the Galapagos, which traced the effects of a significant El Niño event.

Discussion

The results of my explorations of this large range of data is that despite the gaps, there appears to be a correlation between small clutches, protracted parental care and overall parental investment, allowing the young to stay around in their natal territory with their parents. It is too early to say with any certainty whether this promotes the survival of the immatures, but if we are ever to understand the differences between SHTR and NHTE Life Histories, then we need to know more about the post-fledging part of a species' biology. So many of the studies that I read stopped at the point when the nestlings left the nest, breeding success was judged in terms of young fledged, and not even followed to independence, when that would have been

Table 7 Non-cooperatively breeding species from tropical and south temperate regions in which young birds spend at least six months in their parent's territory or with their parents. All species are resident. Abbreviations as in Table 3.

Species	Mass (g)	TWP (d)	Reference
Central and South America			
<i>Myrmotherula longipennis</i> Long-winged Antwren	9	240	Jullien & Thiollay (1998)
<i>Myrmotherula axillaris</i> White-flanked Antwren	8	350	Jullien & Thiollay (1998)
<i>Myrmotherula menetriesii</i> Grey Antwren	9	> 365	Jullien & Thiollay (1998)
<i>Microrhopias quixensis</i> Dot-winged Antwren	8	365	Greenberg & Gradwohl (1985)
<i>Phaenostictus mcleannani</i> Ocellated Antbird	50	> 365	Willis 1973
<i>Phlegopsis nigromaculata</i> Black-spotted Bare-eye	45	> 365	Skutch (1996a)
<i>Thamnomanes ardesiacus</i> Saturnine Antshrike	18	> 365	Jullien & Thiollay (1998)
<i>Phacellodromus rufifrons</i> Common Thornbird	25	> 365	Thomas (1983), Skutch (1996a)
<i>Furnarius rufus</i> Rufous Hornero	58	270	Fraga (1980)
<i>Pseudoseisura gutturalis</i> White-throated Cachalote	—	300	Hudson (1920)
<i>Megarhynchus pitangua</i> Boat-billed Flycatcher	70	240	Skutch (1951, 1960)
<i>Mimus saturninus</i> Chalk-browed Mockingbird	60	210	Fraga (1985)
<i>Tangara guttata</i> Speckled Tanager	20	300	Skutch (1954)
Africa			
<i>Hirundo fuligula</i> Rock Martin	22	270	Keith et al. (1992)
<i>Bleda eximia</i> Green tailed Bristle-bill	42	240-270	Brosset & Erard (1986)
<i>Phyllastrephus icterinus</i> Icterine Greenbul	20	> 365	Brosset & Erard (1986)
<i>Phyllastrephus xavieri</i> Xavier's Greenbul	26	> 365	Brosset & Erard (1986)
<i>Terpsiphone batesii</i> Bate's Paradise Flycatcher	16	270	Urban et al. (1997)
<i>Coracina caesia</i> Grey Cuckoo-shrike	50	300	Maclean 1993
<i>Coracina pectoralis</i> White-breasted Cuckoo-shrike	58	300	Maclean 1993
<i>Dryoscopus senegalensis</i> Red-eyed Puffback	27	300	Brosset & Erard (1986)
<i>Dryoscopus cubla</i> Black-backed Puffback	27	300	Maclean 1993
<i>Laniarius funebris</i> Slate-coloured Bou-bou	47	300	Sonnenschein & Reyer (1984)
<i>Malaconotus blanchoti</i> Grey-headed Bush-shrike	77	300	Maclean (1993)
<i>Bias flammulatus</i> African Shrike-flycatcher	31	300	Brosset & Erard (1986)
<i>Bias musicus</i> Black-and-white Shrike-flycatcher	24	365	Brosset & Erard (1986)
<i>Platysteira cyanea</i> Brown-throated Wattle-eye	15	300	Brosset & Erard (1986)
<i>Platysteira blissetti</i> Red-cheeked Wattle-eye	11	300	Brosset & Erard (1986)
<i>Batis capensis</i> Cape Batis	12	365	Broekhuysen 1958
<i>Batis minima</i> Verreaux's Batis	10	365	Brosset & Erard (1986)
<i>Batis molitor</i> Chinspot Batis	11	365	Urban et al. (1997)
<i>Batis poensis</i> Lawson's Batis	9	365	Brosset & Erard (1986)
<i>Batis senegalensis</i> Senegal Batis	10	365	Urban et al. (1997)
<i>Batis soror</i> East Coast Batis	10	365	Urban et al. (1997)
<i>Fraseria cinerascens</i> White-browed Forest Flycatcher	17.5	300	Brosset & Erard (1986)
<i>Myrmecocichla formicivorus</i> Southern Anteater Chat	49	300	Earlé & Herholdt (1986, 1988)
<i>Neocossyphus finschii</i> Finsch's Flycatcher-thrush	38	300	Brosset & Erard (1986)
<i>Alethe fuelleborni</i> White-chested Alethe	49	365	Brosset & Erard (1986)
<i>Hylota australis</i> Southern Hylota	12	300	Urban et al. (1997)
<i>Apalis rufogularis</i> Buff-throated Apalis	9	> 365	Brosset & Erard (1986)
<i>Ploceus bicolor</i> Forest Weaver	33	300	Maclean (1993)
<i>Lamprotornis purpuropterus</i> Ruppell's Long-tailed Starling	90	> 365	Dittami (1987)
Seychelles Islands			
<i>Copsychus sechellarum</i> Seychelles Magpie Robin	23	294	Komdeur (1996)
New Zealand			
<i>Notiomystis cincta</i> Stitchbird	37	> 365	I. Castro pers. comm.
<i>Mohua novaeseelandiae</i> Brown Creeper	12	270	Maclean & Gill (1988)
Australia			
<i>Menura novaehollandiae</i> Superb Lyrebird	900	270	Lill (1986)
<i>Meliphaga brevirostris</i> Brown-headed Honeyeater	14	>365	Boehm (1968)
<i>Orthonyx spaldingii</i> Chowchilla	185	> 365	Frith et al. (1997)

quite possible. The data I have presented demonstrate that passerine species of the tropics and the southern continents do look after their young for a longer time, but do not explain the origin of the differences between SHTR and NHTE species in the times to independence and dispersal. It is useful to consider these two measures separately.

The longer breeding season in SHTR regions may allow a more relaxed schedule of nesting and re-nesting, without the pressure to moult before migrating and before the onset of the northern winter means that food becomes scarce. We do not yet have enough information on nesting/re-nesting schedules in relation to the care of fledglings to be able to explore this thoroughly. I suggest that the extended Time to Independence is possible because females do not hurry to re-nest as soon after the first brood hatches as many NHTE species appear to do. Ricklefs (1969) made this point many years ago, from a small sample, but no modern survey has revisited it. For example, in *Malurus* spp., the interval between successive clutches is 50-60 days or longer, by which time the first brood is more or less independent. Langen (2000) compared the duration of offspring dependence (Time to Independence) between species that are regularly cooperative breeding, occasionally cooperative breeding and those that do not breed cooperatively. He found that the duration of post-fledging offspring care was significantly longer in species that regularly breed cooperatively. However, he did not look for variation within his sample of non-cooperatively breeding species, for which he calculated a mean duration for post-fledging care of 27.3 days, with a high level of variability. This would be expected from a sample that included north temperate species with short periods of post-fledging care and tropical and south temperate species with much longer duration. Langen considered that the longer period of post-fledging offspring care in cooperatively breeding species occurs because the additional care providers reduce the cost of parenting. However, this does not explain the extended post-fledging care in many other species of tropical and temperate birds. It may be more useful to see cooperative breeding as a result of extended post-fledging parental care, not as part of its cause.

In many species where the young stay with their parents long after independence, only one brood is produced. This was noted by both Fogden (1972) and Jullien & Thiollay (1998). Fogden commented (1972)

‘... 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.’ Similarly, for the members of mixed species flocks of insectivores in the understorey of Neotropical forests, Jullien & Thiollay (1998) 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...’. 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. A detailed study of the Song Wren *Cyporhinus phaeocephalus* in Panama found that 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. The mean interval between nesting attempts for those few individuals that re-nested after fledging young was 88.5 days (range 63-130 days), compared with intervals of 6, 10 and 11 days for three north temperate species of wren (*Campylorhynchus brunneicapillus*, *Troglodytes aedon* and *Thryothorus ludovicianus* (Robinson et al. 2000). To some extent, this also occurs with species of Australia and southern Africa, where females may have time to re-nest after one or two failures, and still produce a successful clutch.

One key to the difference between northern and southern life histories lies in the greater area of land in the higher latitudes of the Northern hemisphere. Most migration has evolved as a strategy to cope with the severe winters, but it imposes severe time constraints — a short breeding season and the need for breeders to get themselves and their young to a stage where they are ready to migrate in Autumn, with new feathers and sufficient reserves of fat to get them to their destination. Migration is not often listed as one of the factors responsible for differences between southern and northern life histories, but because the majority of tropical and southern passerines do not migrate, its absence is an important factor. Hockey (2000) has shown that the correlation of migration with latitude holds for Africa with the proportion of species that is migratory closely related with latitude and to the average temperature of the coldest month of the year. In the south-west cape of South Africa at c. 34°S, 88% of breeders are resident, whereas at latitudes above 60°N, fewer than 40% of

breeders are resident (see Hockey 2000, Fig. 2). There are many nomads, mainly in arid and seasonally arid areas north and south of the equator, but details of their life histories are very poorly known.

A significant difference between NHTE and SHTR species is that many of the SHTR species for which data are available are resident all year round in the territory in which they breed. These territories are clearly able to support the pair and their offspring (from a small clutch) throughout the year. In NHTE regions, especially those susceptible to severe winters, fewer species live all year round in a territory that provides all their needs. Of the species that do not migrate, many join wandering winter flocks. The breeding territories may be such that, with the prevailing large clutches, they provide sufficient resources for the breeding pair and their current brood of nestlings, but not enough for a fledged first brood who must leave and find food elsewhere. Most of these ideas are speculative, because there is so little information about what happens to nestlings after they become independent.

Another key to the differences may lie in phylogeny. I have not attempted to consider that in this preliminary survey since the majority of passerine species in Australia and South America are only distantly related to those of Europe, Asia and Africa. It was demonstrated by Cockburn (1996) that cooperative breeding is a basic trait in the Corvida, lost secondarily in some groups in some families. There are other similar groups, such as the Asiatic babblers (Tribe Timaliini in the Family Sylviidae), in which cooperative breeding is common. These patterns suggest that the social aspects of delayed dispersal may involve phylogeny as well as ecology. In their recent review of explanations of cooperative breeding, Hatchwell & Komdeur (2000) have suggested that the distinction between ecological constraint and life history hypotheses for the occurrence of cooperative breeding are artificial, and that a broad hypothesis incorporating ecological and life history traits stands a more realistic chance of identifying the selection pressures resulting in cooperative breeding. Delayed dispersal is not restricted to cooperative breeding species. For most of the last 35 years, work has focused on helping and the benefits accrued from helping to rear relatives. When we look at cooperative breeding in the broader context, it is part of the pattern of tropical and southern life histories, with high survival and extended parental care. It is part of a continuum of extended parental care — many species stay up to the next breeding season, some stay longer and help.

Conclusion

This study indicated some major gaps in available information, which makes it hard to recognise patterns but at the same time suggests areas for future research:

(1) So many species are virtually unknown, especially in South America. They may be known as part of a community, but individual life histories are unknown.

(2) Migrants and nomads in SHTR regions are virtually unknown, on all continents, but I am particularly aware of these gaps in Australia, where studies are concentrated round major cities (Clarke 1996).

(3) India is not a southern continent, and so I have not considered it a great deal, but there are hundreds of little known species, including many babblers and laughingthrushes, all of which seem to live in groups.

(4) Studies do not persist long enough. Breeding Success data is quoted when young fledge, but the stages from fledging to independence and from independence to first breeding are obviously of great importance in shaping life histories and that is not widely recognised. This is a field we must stop ignoring in Australian (and southern hemisphere) Ornithology. We have followed established paths based on studies of the life histories of northern birds, studying breeding biology from laying to fledging and stopping at that point. What happens after that is also a fundamental part of the life history. It is not easy because one has to study banded birds, know the territories of breeding pairs, and keep track of young birds all year round.

(5) It is not yet possible to compare the reproductive effort expended by males and females between northern and southern habitats. It is possible that by increased investment in a few young, total reproductive effort is reduced for tropical and southern species, which may contribute to the observed higher survival of adults (Russell & Rowley 2000).

Some of this apparently academic life history theory is relevant to management. Many endangered species have clutch sizes of one or two; high adult survival may give apparently respectable adult populations, but if fecundity is low, losses are not replaced. The whole process depends on the high survival of adults and juveniles and if habitat clearing and management techniques upset the vital juvenile and adult survival links in the chain, we ask our birds to do something they have not evolved to do — reproduce at high rates to make good the losses.

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Appendix 1 Values of juvenile survival (Js_{ur}; %) from published and unpublished sources. Species marked with an asterisk are migratory or nomadic. Abbreviations: NAm, North America; CSAm, Central and South America; SAm, South America; NZ, New Zealand; Aust, Australia; Galap, Galapagos Is.; Seych, Seychelles Islands; P. Rico, Puerto Rico.

Species	Wt (g)	Location	Js _{ur} (%)	Reference
<i>Junco hyemalis</i> Dark-eyed Junco*	20.0	NAm	10	Wolf et al. 1988
<i>Parus palustris</i> Marsh Tit	11.9	Europe	10	Smith 1993
<i>Junco phaeotus</i> Yellow-eyed Junco*	20.0	NAm	11	Sullivan 1989
<i>Turdus merula</i> Blackbird	100.0	Europe	11	Magrath 1991
<i>Zonotrichia leucophrys nuttalli</i> Nuttall's Sparrow	31.0	NAm	12	Baker et al. 1981
<i>Passerculus sandwichensis</i> Savannah Sparrow	24.0	NAm	14	Ross & McLaren 1981
<i>Alauda arvensis</i> Skylark	42.7	Europe	15	Delius 1965
<i>Parus cristatus</i> Crested Tit	11.5	Europe	15	Ekman et al. 1981
<i>Gymnorhinus cyanocephalus</i> Pinyon Jay	112.0	NAm	16	Marzluff & Balda 1992
<i>Parus major</i> Great Tit	18.9	Europe	22	Dhondt 1979
<i>Perisoreus canadensis</i> Grey Jay	75.0	NAm	26	Strickland & Ouellet 1993
<i>Dendroica discolor</i> Prairie Warbler*	8.0	NAm	32	Nolan 1978
<i>Sitta europaea</i> European Nuthatch	22.0	Europe	33	Matthysen 1988
<i>Aphelocoma ultramarina</i> Mexican Jay	124.0	NAm	34	Brown 1982
<i>Aphelocoma coerulescens</i> Florida Scrub Jay	80.0	NAm	35	Woolfenden & Fitzpatrick 1984
<i>Dolichonyx oryzivorus</i> Bobolink*	25.0	NAm	35	Wittenberger 1978
<i>Melospiza melodia</i> Song Sparrow	21.0	NAm	40	Smith 1988
<i>Sitta pygmaea</i> Pygmy Nuthatch	10.6	NAm	44	Sydemann 1989
<i>Pyrrhonorax graculus</i> Alpine Chough	210.0	Europe	50	Delestrade & Stoyanov 1995
<i>Turdoides squamiceps</i> Arabian Babbler	74.0	Israel	52	Zahavi 1990
<i>Troglodytes aedon</i> House Wren	12.0	CSAm	10	Young 1994
<i>Malurus leucopterus</i> White-winged Fairy-wren	7.6	Aust	10	Rowley & Russell 1995
<i>Geospiza conirostris</i> Large Cactus Finch	28.0	SAm	11	Grant & Grant 1989
<i>Acanthisitta chloris</i> Rifleman	6.3	NZ	17	Sherley 1994
<i>Petroica australis</i> South Island Robin	22.0	NZ	17	Powlesland 1983
<i>Quelea quelea</i> Quelea*	18.0	Africa	22	Ward 1965
<i>Taeniopygia guttata</i> Zebra Finch	13.0	Aust	22	Zann & Runcimann 1994
<i>Mohoua ochrocephala</i> Yellowhead	15.0	NZ	22	Elliott 1996
<i>Xenicus gilviventris</i> Rock Wren	15.6	NZ	22	Michelsen-Heath 1989
<i>Malurus cyaneus</i> Superb Fairy-wren	9.4	Aust	25	Rowley & Russell 1997
<i>Cyanocorax sanblasiana</i> San Blas Jay	109.0	CSAm	26	Hardy et al. 1981
<i>Manorina melanophrys</i> Bell Miner	33.0	Aust	30	Clarke & Heathcote 1990
<i>Malurus pulcherrimus</i> Blue-breasted Fairy-wren	9.4	Aust	30	I. Rowley & E. Russell unpubl. data
<i>Eopsaltria georgiana</i> White-breasted Robin	17.0	Aust	31	R. Brown & M. Brown unpubl. data
<i>Malurus splendens</i> Splendid Fairy-wren	10.6	Aust	31	Russell & Rowley 1993
<i>Passer melanurus</i> Cape Sparrow	29.6	Africa	32	Rowan 1966
<i>Zosterops lateralis</i> Capricorn Silvereye	11.0	Aust	32	Wilson & Kikkawa 1988
<i>Nesomimus parvulus</i> Galapagos Mockingbird	56.2	Galap	35	Curry & Grant 1990

Continued next page

Appendix 1 Continued.

Species	Wt (g)	Location	Jsur (%)	Reference
<i>Sericornis frontalis</i> White-browed Scrubwren	19.0	Aust	35	Magrath & Yezerinac 1997
<i>Hylophylax naevioides</i> Spotted Antbird	18.0	CSAm	36	Willis 1972
<i>Pomatostomus superciliosus</i> White-browed Babbler	40.5	Aust	38	Cale 1999
<i>Malurus elegans</i> Red-winged Fairy-wren	9.9	Aust	41	Russell & Rowley 2000
<i>Vireo latimeri</i> Puerto Rican Vireo	11.5	P. Rico	41	Woodworth et al. 1999
<i>Gymnophithys leucaspis</i> Bicolored Antbird	32.0	CSAm	42	Willis 1967
<i>Turdoides striatus</i> Jungle Babbler	66.0	India	43	Gaston 1978a
<i>Corvinella corvina</i> Yellow-billed Shrike	65.0	Africa	44	Grimes 1980
<i>Donacobius atricapillus</i> Black-capped Donacobius	53.0	SAm	44	Kiltie & Fitzpatrick 1984
<i>Copsychus sechellarum</i> Seychelles Magpie Robin	23.0	Seych	45	Komdeur 1996
<i>Turdoides caudatus</i> Common Babbler	35.0	India	48	Gaston 1978b
<i>Plocepasser mahali</i> White-browed Sparrow weaver	48.6	Africa	48	Lewis 1982
<i>Corcorax melanorhamphos</i> White-winged Chough	371.7	Aust	50	Rowley 1978
<i>Campylorhynchus griseus</i> Bicolored Wren	42.4	SAm	54	Austad & Rabenold 1985
<i>Cracticus nigrogularis</i> Pied Butcherbird	114.0	Aust	59	Robinson 1994
<i>Callaeas cinerea</i> Kokako		NZ	60	I. Flux pers. comm.
<i>Agelaius xanthomus</i> Yellow-shouldered Blackbird	41.0	P. Rico	66	Post 1981
<i>Acanthiza reguloides</i> Buff-rumped Thornbill	8.2	Aust	95	Bell & Ford 1986
<i>Petroica australis longipes</i> North Island Robin	22.0	NZ	73	Armstrong et al. (in press)
<i>Acrocephalus sechellensis</i> Seychelles Warbler	17.0	Seych	80	Komdeur 1994