THE EFFECT OF ANNUAL RAINFALL ON THE SURVIVAL RATES OF SOME AUSTRALIAN PASSERINES

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Abstract.—The survival rates of 18 species of wide-ranging Australian passerines were calculated by using recapture data provided by the Australian Bird Banding Scheme for birds older than one year. On average, birds living in relatively lower rainfall areas (<760 mm annually) lived 15% longer than birds living in higher rainfall areas (>760 mm). Out of 18 species examined, only three do not conform with this general trend.

EL EFECTO DE EL PATRÓN DE LLUVIA ANUAL EN LA TASA DE SUPERVIVENCIA DE ALGUNOS PASERINOS AUSTRALIANOS

Sinopsis.—La tasa de supervivencia de 18 especies de paserinos Australianos fue calculada utilizando datos de recaptura provistos por la oficina de Anillaje Australiana para aves de más de un año. En promedio, las aves que viven en áreas de menos lluvia (<760 mm anuales) vivieron un 15% más que las aves que viven en áreas más lluviosas (>760 mm). De las 18 especies estudiadas, tan solo tres no cayeron dentro de esta tendencia.

The survival of various organisms, including birds, is related to body mass (Calder 1984, Dobson 1990), although other life history traits may have a considerable influence on survival (Stearns 1992) Body mass of individuals is positively correlated with survival when considered at an interspecific level (Calder 1984), although within species the picture is less clear. Survival is also related to clutch size and total reproductive effort, both of which vary geographically and between habitats (e.g., Dobson 1990). Thus, life histories (i.e., survival and fecundity schedules and their inter-relations) should represent an adaptation to a species' strategy of life in a particular habitat or climate. However, little work has been done to compare survival of birds in relation to climate. It is generally believed that tropical birds live longer than those of temperate regions (Ricklefs 1973), but there appear to be no studies of survival of birds in relation to rainfall. For example, no data on survival are provided for any of the Palearctic desert passerines which are dealt with in Cramp (1988).

The large amount of data accumulated by bird-banding schemes in different countries provides a unique resource for monitoring the survival

rates of a broad range of bird species, and enables a comparison of sur-
vival in different habitats (Dobson 1990). In a previous paper (Yom-Tov
et al. 1992), we used the extensive data stored at the Australian Bird
Banding Scheme (ABBBS) to compare the survival rate of some Austra-
lian passerines to those of British passerines, and the survival rates of the
"old endemics" among the Australian birds to the "new invaders". We
found that Australian passerines tend to live longer than British ones,
with no difference between "old endemics" and "new invaders." Many
of these bird species inhabit large areas in Australia where climate, par-
ticularly rainfall, varies greatly. In this paper we used the same source of
data to compare the survival rates of birds of the same species which live
in high and low rainfall regimes.

METHODS

The data in this analysis were provided by the Australian Bird Banding
Scheme, Australian Nature Conservation Agency, Canberra. They origi-
nated from intensive banding studies, which produced large numbers of
subsequent recaptures, and from opportunistic banding, which produced
fewer recaptures, between 1962–1990. We used only recaptures (not re-
coveries of birds found dead), as more of these data were available. Eight-
een species for which a large number of recapture data were readily avail-
able were selected for analysis (Table 1). Only birds older than 1 yr at
banding were used in the analysis, but recaptures that occurred less than
5 mo after banding were not included, as they might have biased the
estimates of survival. Body mass of all species was less than 325 g, with 14
weighing 6–25 g, and four weighing 60, 90, 275 and 323 g, respectively.
They include 16 old endemics, one new invader (Red-browed Firetail,
Emblema temporalis) and a European introduction (Blackbird, *Turdus mer-
ula*).

The majority of the data came from four regions in Australia: (1) the
southwestern corner of Western Australia (WA); (2) southern South Aus-
tralia; (3) the temperate areas of Victoria, Tasmania, and New South
Wales (NSW); and (4) eastern Queensland (Fig. 1). Most specimens from
WA came from localities less than 100 km from the coast of the Indian
Ocean, but there were about 63 from isolated localities further inland.
All specimens from South Australia came from localities less than 120 km
from the coast and those from NSW, Victoria, and southern Queensland
came from localities less than 300 km from the coast. Hence, most of our
data came from the Bassian region. For each locality we assigned mean
annual rainfall measured at the closest meteorological station as given in
Wernstedt (1972). This source provides long-term averages of monthly
and annual precipitation for more than 300 weather stations throughout
Australia.

A comparison of species within the Australian data set required an
index of longevity derived from the ringing data with a minimum of as-
sumptions. We started, therefore, by determining the time elapsed be-
tween the date of banding and date of the last recapture of each individ-

TABLE 1.   The total number of years of banding and recapture of a species and the number of sites in each rainfall regime.

Species	Semi-arid areas			Mesic areas		
	Band-ing, years	Recap-ture, years	No. sites	Band-ing, years	Recap-ture, years	No. sites
Blackbird,						
Turdus merula	10	9	27	6	6	6
Eastern Yellow Robin,						
Eopsaltria australis	7	6	20	5	5	28
Golden Whistler,						
Pachycephala pectoralis	7	8	18	5	5	21
Grey Shrike-thrush,						
Colluricincla harmonica	8	9	15	6	5	13
Grey Fantail,						
Rhipidura fuliginosa	7	7	19	7	7	26
Superb Fairy-Wren,						
Malurus cyaneus	12	12	45	3	4	21
White-browed Scrubwren,						
Sericornis frontalis	9	8	33	5	8	34
Striated Thornbill,						
Acanthiza lineata	11	10	27	3	3	10
Brown Thornbill,						
Acanthiza pusilla	7	6	28	6	5	26
Yellow-faced Honeyeater,						
Lichenostomus chrysops	7	6	16	5	5	12
White-naped Honeyeater,						
Melithreptus lunatus	8	7	12	5	5	5
Brown Honeyeater,						
Lichmera indistincta	4	4	10	6	5	14
New Holland Honeyeater,						
Phylidonyris novaehollandiae	10	11	41	7	6	23
Eastern Spinebill,						
Acanthorhynchus tenuirostris	10	9	24	6	7	26
Silvereye,						
Zosterops lateralis	11	10	40	9	7	41
Red-browed Firetail,						
Emblema temporalis	11	11	18	5	5	22
Australian Magpie,						
Gymnorhyna tibicen	11	8	29	8	7	21
Pied Currawong,						
Strepera graculina	6	5	6	5	3	6

ual (DLR). When the distribution of the banding date-last recapture interval is plotted for each species it gives, not surprisingly, a right-skewed histogram. Average longevity alone would give undue weight to a few long-lived individuals. In theory one might expect that DLR should have an exponential distribution with variance proportional to mean squared. The usual transformation would be logarithmic, but we found that this left us with rather strongly skewed residuals. We suspect that this is because although the mean-variance relationship is consistent with expo-
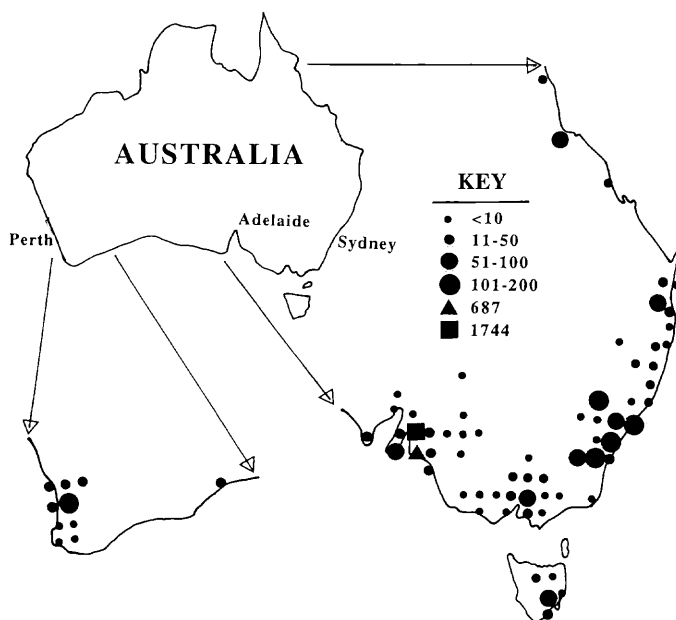
FIGURE 1.   Localities of the birds in this study, organized by one degree square blocks. The
    number of retraps in each locality is indicated by dots of different size (see key).

nential distribution there may be a distortion at low DLR values. In any
case we followed the suggestion of Armitage and Berry (1987:363) for
these kinds of data and used a reciprocal transformation. For all species
in our sample this transformation of the individual band longevity gives
a reasonably normal distribution, whose mean is referred to as the specific
death rate (SDR) in Table 2. The reciprocal of the SDR is the harmonic
mean of the survival times for each species (in years).

    After carrying out statistical analysis using the GLM procedure of Min-
itab, we checked the distribution of the residuals, and plotted them
against the fitted values to check for heterogeneity of variance. Although
a slight right skew remains in the residuals even after reciprocal transfor-
mation, it is unlikely to have affected the results significantly. In no case
did we find any heterogeneity in the variance of SDR.

    Although we used only species with relatively large numbers of recap-
tures, the data were unevenly distributed between years and localities.
Typically there were extensive recaptures for a number of years, followed
by long periods with little additional data, with a possible one or more
additional periods of many recaptures. This pattern reflects the passing
interest or temporary residency of an individual or group of banders in
a particular species. Hence, our study is sensitive to which studies are
included in it. However, the criterion we used for selecting a species to
participate in this study was that there were a relatively large number of

retraps of this species, and no species was excluded for any other reason. Another source of bias in our data is that some of them come from birds that were banded as part of a study of colored-banded birds which are primarily re-encountered by sightings, and are not recaptured at random. Such resightings are rarely reported to the ABBBS (Ian Rowley, pers. comm.) and might cause our estimated survival rates to be too low. This bias affects at least two species in our study (White-browed Scrubwren, *Sericornis frontalis* and Superb Fairy-wren, *Malurus cyaneus*). Some of the species in our sample are migratory. However, because we compare populations of the same species in two rainfall regimes, this factor should not affect our results.

RESULTS

Most specimens of all species (more than 98%) were caught less than 10 km from their place of banding, suggesting that these birds do not travel large distances, and even the migratory species are philopatric. This is apparently also an indication of the sparse distribution of bird banders in Australia. There was no correlation between sample size and the coefficient of variation of SDR of the species concerned.

Rainfall at the localities from which the data came were not evenly distributed and had a bimodal distribution, with no localities with mean annual rainfall between 745–840 mm. We therefore divided our sample into two groups, according to mean annual rainfall: below 760 mm (semiarid: mean = 513 mm, SD = 150, 185 localities); and above 760 mm (mesic: mean = 1095 mm, SD = 211, 79 localities).

Eighteen species were found that were ringed at a locality for at least 4 yr and for which there were more than 20 observations in both the semiarid and mesic rainfall areas. (Table 1).

Overall, the SDR was lower in semi-arid areas, so that on average these birds live longer, surviving on average about 1.12 yr after banding, compared with about 0.97 yr in mesic areas (Table 2). Of the 18 species included, 15 had longer SDR's in semi-arid areas, and 3 did not. Simply applying a sign test rejects the null hypothesis that they are equally likely to live longer in either place ($P < 0.001$). This was confirmed by analysis of variance (for species: $F_{1,17} = 5.31$, $P = 0.0001$; for rain: $F_{1,17} = 9.06$, $P = 0.0001$). There was a fairly strong interaction between species and rainfall in determining SDR ($F_{1,17} = 2.34$, $P = 0.002$), meaning that the difference between low and high rainfall varies between species. Inspection of the interaction coefficients showed that the significance of the interaction was probably attributable to three species that have positive coefficients significantly greater than zero. These were the ones where the mean SDR was higher in semi-arid areas (Table 2), namely the Eastern Yellow Robin (*Eopsaltria australis*), the Eastern Spinebill (*Acanthorhynchus tenuirostris*), and the Brown Honeyeater (*Lichmera indistincta*). Reanalysis without these species shows no interaction ($F_{1,14} = 1.49$, $P = 0.107$), and a strong effect of the rainfall regime ($F_{1,14} = 57.62$, $P =$

TABLE 2. Sample size, number of years for which there are recapture data, body mass (from Yom-Tov 1987), and mean specific death rate (SDR). See Table 1 for scientific names.

| Species | No. of years | Body mass (g) | Specific death rate | | | | | |
| | | | Semi-arid areas | | | Mesic areas | | |
			n	Mean	SD	n	Mean	SD
Blackbird	10	90	99	0.90	0.53	27	0.91	0.43
Eastern Yellow Robin	10	20	41	1.01	0.49	80	0.95	0.38
Golden Whistler	8	24	64	0.78	0.44	52	0.88	0.43
Grey Shrike-thrush	11	60	35	0.73	0.49	26	0.96	0.60
Grey Fantail	18	8	31	0.91	0.50	42	1.00	0.54
Superb Fairy-Wren	13	9	301	0.93	0.49	69	1.23	0.39
White-browed Scrubwren	10	12	116	0.95	0.47	110	1.08	0.39
Brown Thornbill	13	10	106	0.95	0.41	66	1.02	0.43
Striated Thornbill	19	6	272	0.80	0.52	25	1.02	0.31
Yellow-faced Honeyeater	10	14	149	0.82	0.40	26	1.06	0.51
White-naped Honeyeater	8	13	101	0.82	0.40	26	0.97	0.38
Brown Honeyeater	8	8	45	1.03	0.38	41	0.97	0.43
New Holland Honeyeater	11	18	643	0.99	0.48	143	1.12	0.45
Eastern Spinebill	10	10	189	0.95	0.47	94	0.93	0.42
Silvereye	13	11	501	0.83	0.41	147	1.03	0.44
Red-browed Firetail	12	10	181	1.04	0.48	87	1.10	0.36
Australian Magpie	27	323	58	0.83	0.63	54	1.13	0.58
Pied Currawong	28	275	150	0.57	0.34	20	0.89	0.55
All			3187	0.91	0.48	1234	1.03	0.44

0.0001), as well as the expected difference between species ($F_{1,14}$ = 6.22, $P = 0.0001$).

The average duration of retraps was 9.6 yr in semi-arid sites and 5.4 yr in mesic sites, and this may have produced a bias in the form of longer survival in semi-arid areas. However, there was no correlation between SDR and the number of years of retraps across species and areas, neither there was a correlation between the ratio of the number of years of retraps in semi-arid and mesic areas and the ratio between SDR in these areas for each species. This is logical, because the average survival of birds in our study was only about a year. Hence, the number of retrap years did not seem to affect the results of this study.

We scrutinized the distributions of the three species that show a different pattern from the rest in order to examine their validity as counter instances. For the Eastern Spinebill, the data suggest that while most individuals live up to 3 yr after banding in both rainfall regimes, only in

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FIGURE 2. Survival times (SDR) in low and high rainfall areas. (a) The Brown Honeyeater *Lichmera indistincta*. The difference in between the two rainfall regimes is mainly due to a long tail in high rainfall areas. (b) The Eastern Spinebill *Acanthorhynchus tenuirostris*. The large number of short-lived birds in low rainfall areas obscures the fact that only in such areas do significant numbers of birds live beyond 3 years.

a) Brown Honey Eater

semi-arid

mesic

b) Eastern Spinebill

semi-arid

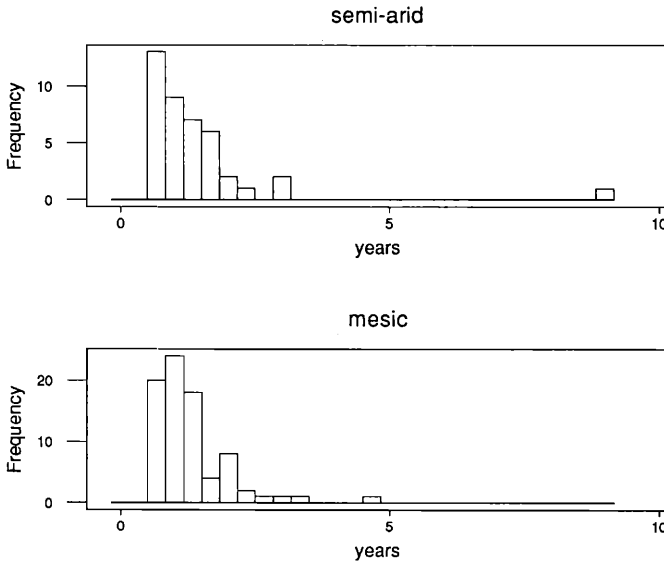mesic
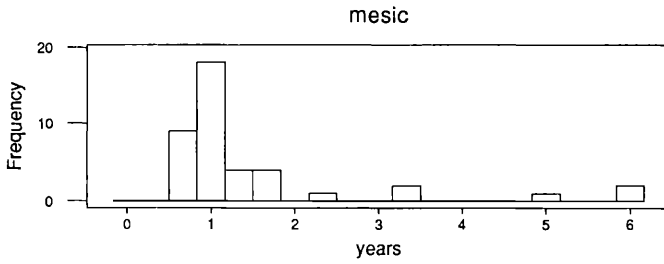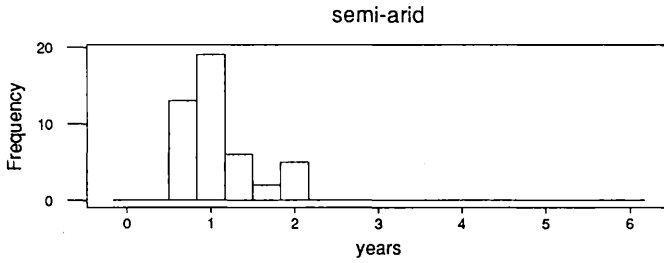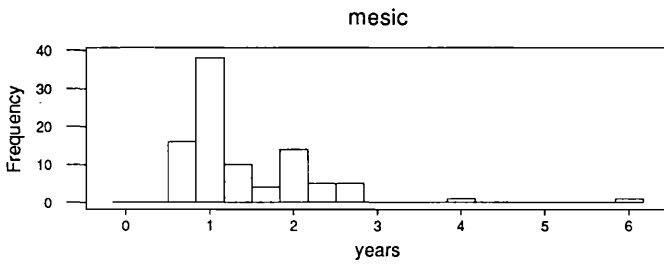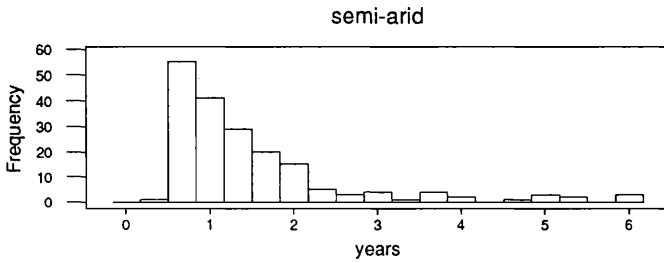
c) Eastern Yellow Robin

semi-arid

mesic

FIGURE 2.   (c) The Eastern Yellow Robin *Eopsaltria australis*. There is no evidence of a
difference between high and low rainfall areas.

semi-arid areas do significant numbers live for longer (Fig. 2b). This spe-
cies was studied by McFarland and Ford (1987) in an area where mean
annual rainfall is more than 2000 mm (mesic area in our analysis). Their
data were not available to us, and the published data cannot simply be
added to our data, because the precise time to last recapture is not given.
On the other hand, we cannot use their methods as we do not know the
numbers ringed and never seen again for any data besides theirs. Their
Table 2 shows that indeed in their study many birds lived 3, 4, 5 and more
years, and on the face of it the birds in their data set lived longer than
the ones we have recorded, especially for mesic areas. As a rough analysis
of this we carried out contingency analyses (Table 3) examining the pro-
portions of birds caught at least once after banding that were still alive
at 3 yr after banding. Table 3a shows that McFarland and Ford's data are
different from our original data set from mesic areas, but Table 3b shows
that if we pool their data with ours from mesic areas for survival to 3 yr,
there is still no significant relationship with rainfall. Thus, there is no
reason to class the Eastern Spinebill as a counter instance to the general
result, though it does not conform to it either. In the other two species,
although there is a slight tendency for longer recovery times in mesic
rather than semi-arid areas, the evidence does not appear to be strong

TABLE 3.   A simple analysis of the proportion of Eastern Spinebills still alive at 3 years or more after banding shows (a) that McFarland and Ford's (1987) data are different from ours ($\chi^2 = 10.739$, df = 2, $P < 0.005$), but that when combined with our data for mesic areas (b) there is no effect of rainfall on proportion of birds seen more than 3 yr after ringing ($\chi^2 = 0.32$, df = 1, ns).

(a)

Study and area		Not alive >3 yr	Alive >3 yr	Total
This study, semi-arid	Observed	172	17	189
	Expected	170.17	18.83	
This study, mesic	Observed	92	2	94
	Expected	64.64	9.36	
McFarland and Ford	Observed	197	32	229
	Expected	206.19	22.81	
Total		461	51	512

(b)

Study and area		Not alive >3 yr	Alive >3 yr	Total
This study, semi-arid	Observed	172	17	189
	Expected	170.17	18.83	
This study mesic +	Observed	289	34	323
McFarland and Ford	Expected	290.83	32.17	
Total		461	51	512

(Figs. 2a, c). In the remaining 15 species, the tendency for birds living in semi-arid areas to survive longer after banding is statistically strong. The origin of the birds does not appear to affect their survival rates, as both the new invader and the European introduction behaved similarly to most old endemics.

DISCUSSION

Our analyses show that birds living in semi-arid areas in Australia live on average 15% longer than those in more mesic areas. This might be related not only to the amount of annual rainfall at a particular locality, but also (or even primarily) to higher seasonality in primary productivity in wetter areas (Nix 1976, Pyke 1983, Woinarski and Cullen 1984). In Australia, the least seasonal areas are inland from the coastal ranges (i.e., areas of moderate, not high rainfall, such as our semi-arid areas). Ford et al. (1988) argued that low seasonality led to the high incidence of cooperative breeding, and by implication, higher adult survival in such semi-arid areas. We do not have data on seasonality of the localities from which our data came, but our results support Ford et al. (1988) conclusions: birds from semi-arid areas survive longer than those of mesic ones.

Several authors have shown that there is a trade-off between fecundity and adult survival (reviewed by Stearns 1992). Interspecific comparisons indicate that clutch size and annual productivity (clutch size × number

of broods × success rate) are inversely related to adult survival (Bennet
and Harvey 1988; Ekman and Askenmo 1986; Martin and Clobert 1996;
Saether 1988). In many multibrooded Australian species clutch size shows
little variation. In Australia, variation in seasonal reproductive effort arises
not through variation in clutch size, but through variation in the number
of nests, which in part depends on the length of the breeding season
(Rowley and Russell 1991). Dobson (1990) has shown that for British
birds, clutch size and, more importantly, the number of times a bird at-
tempts to breed each year, are correlated with adult survival. He found
that among passerines there is a negative correlation between survival
and the number of times a bird attempts to breed in a year, and a positive
correlation between clutch size and survival. Our data do not include the
number of breeding attempts in any of the studied areas, but it is reason-
able to assume that where there is relatively little rainfall, the breeding
season is shorter than in wetter regions, and hence the number of breed-
ing attempts there is smaller. Alternatively it may be that breeding is not
possible at all in some years due to year to year predictability, leading to
some individuals "holding on" for another season before dying. If this
assumption is correct, our results are in agreement with those of Dobson
(1990), in which survival correlates negatively with the number of breed-
ing attempts.

It would be interesting to know whether this difference in longevity is
a phenotypic or genotypic effect. In environments where breeding is
sometimes precluded by drought there may be stronger selection for lon-
gevity than in more seasonal areas. On the other hand, birds that are
unable to breed due to environmental factors may not wear themselves
out in that season and with therefore have a better chance of survival.
There is some evidence that under certain conditions skipping a season
increased lifespan in the Great Tit *Parus major* in Wytham (McCleery et
al. 1996). One would need to study individually marked populations
which have lived through periods of variable rainfall to distinguish these
possibilities.

Finally, we interpreted recapture as equivalent to survival. However, it
is possible that birds in mesic areas are more likely to disperse beyond
the study area and thus be recaptured less than in semi-arid areas, thus
giving the impression that they survive less well than birds inhabiting
semi-arid areas. The sparsity of bird banders in Australia is such that this
interpretation cannot be examined at present.

LITERATURE CITED

ARMITAGE, P., AND G. BERRY. 1987. Statistical methods in medical research. Blackwell Scientific Publications, Oxford, United Kingdom.

BENNETT, P. M., AND P. H. HARVEY. 1988. How fecundity balances mortality in birds. Nature 333:216.

CALDER, W. A. III. 1984. Size, function and life history. Harvard University Press, Cambridge, Massachusetts.

CRAMP, S. ed. 1988. Handbook of the birds of Europe, the Middle East and North Africa, Vol. 5. Tyrant Flycatchers to Thrushes. Oxford University Press, Oxford, United Kingdom.

DOBSON, A. 1990. Survival rates and their relationship to life-history traits in some common British birds. Current Ornithology 7:115–146.

EKMAN, J., AND C. ASKENMO. 1986. Reproductive cost, age-specific survival and a comparison of the reproductive strategies in two European tits (genus *Parus*). Evolution 40:159–168.

FORD, H. A., H. BELL, R. NIAS, AND R. NOSKE. 1988. The relationship between ecology and the incidence of cooperative breeding in Australian birds. Behav. Ecol. Sociobiol. 22: 239–249.

MARTIN, T., AND J. CLOBERT. 1996. Nest predation and avian life history evolution in Europe versus North America: a possible role of humans? Am. Nat. 147:1028–1046.

MCCLEERY, R. H., J. CLOBERT, R. JULLIARD, AND C. M. PERRINS. 1996. Nest predation and delayed cost of reproduction in the Great tit. J. Anim. Ecol. 65:96–104.

MCFARLAND, D. C., AND H. A. FORD. 1987. Aspects of population biology of the Eastern spinebill *Acanthorhynchus tenuirostris* (Meliphagidae) in New England National Park, NSW. Corella 11:52–58.

NIX, H. 1976. Environmental control of breeding, post-breeding dispersal and migration of birds in the Australian region. Pp. 272–305, *in* Proc. 16th Intern. Ornith. Cong. Canberra, Australia.

PYKE, G. H. 1983. Seasonal pattern of abundance of honeyeaters and their resources in heathland areas near Sydney. Austr. J. Ecol. 8:217–233.

RICKLEFS, R. E. 1973. Fecundity, mortality and avian demography. Pp. 366–435, *in* D. S. Farner, ed. Breeding biology of birds. National Academy of Sciences, Washington, D.C.

ROWLEY, I., AND E. RUSSELL. 1991. Demography of passerines in the temperate southern hemisphere. Pp. 22–44, *in* C. M. Perrins, J-D. Leberton, and G. J. M. Hirons, eds. Bird population studies. Oxford University Press, Oxford, United Kingdom.

SAETHER, B.-E. 1988. Patterns of covariation between life-history traits of European birds. Nature 331:616–617.

STEARNS, S. C. 1992. The evolution of life histories. Oxford University Press, Oxford, United Kingdom.

WERNSTEDT, F. L. 1972. World climate. Climatic Data Press. Lemont, Pennsylvania.

WOINARSKI, J. C. Z., AND J. M. CULLEN. 1984. Distribution of invertebrates on foliage in forests of south-eastern Australia. Austr. J. Ecol. 9:207–232.

YOM-TOV, Y. 1987. The reproductive rates of Australian passerines. Australian Wildlife Journal 14:319–330.

———, MCCLEERY, R., AND PURCHASE, D. 1992. The survival rate of Australian passerines. Ibis 134:374–379.