

EFFECTS OF PRIOR RESIDENCE AND AGE ON BREEDING PERFORMANCE IN YELLOW WARBLERS

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ABSTRACT.—Age-related increases in reproductive success could be the result of better survival by successful breeders (survival hypothesis), greater dispersal by unsuccessful breeders (dispersal hypothesis), and/or age-related differences in the ability to compete for breeding opportunities (constraint hypothesis). We used banding and nesting data from four consecutive breeding seasons to examine the effects of prior residency on several indices of breeding performance in Yellow Warblers (*Dendroica petechia*). We compared the breeding performance of returning birds with that of new arrivals, and of individuals between successive breeding seasons. There were no differences in clutch size between new arrivals and returning individuals, nor within individuals between successive breeding seasons. Among males, prior residence had no effect on whether a clutch was started, but among females the number of prior residents that initiated a clutch was higher than expected, and the number of new arrivals that did not was lower than expected. In contrast, there were no differences in laying or hatching date between new arrivals and returning individuals, but within-individual comparisons showed that males bred earlier in successive breeding seasons. Previous reproduction increased subsequent return rates only 1 out of 3 years in both sexes. Returning males were larger than new arrivals, but there were no differences in females. Within-individual size increases between successive breeding seasons occurred in both sexes. These results are consistent with the constraint hypothesis, but the proximate mechanisms by which these differences arise remain to be determined. Received 1 Oct. 1998, accepted 20 Feb. 1999.

Age-related increases in reproductive success have been documented in many bird species (reviewed by Sæther 1990, Forslund and Pärt 1995). Several hypotheses have been proposed to explain this phenomenon. Forslund and Pärt (1995) divided these hypotheses into three groups depending on whether they are based on (1) the gradual appearance or disappearance of certain phenotypes, (2) the lifetime optimization of reproductive effort, or (3) age-related improvements in competence. These three groups of hypotheses are not mutually exclusive.

In the first group of hypotheses, differences in reproductive success among age classes are not viewed as the result of individuals increasing their reproductive success with age, but rather as a result of the elimination of some phenotypes from the population. The probability of breeding may be positively correlated with the likelihood of survival (survival hypothesis) or negatively correlated with the likelihood of dispersal (dispersal hypothesis; e.g., Smith 1981, Nol and Smith 1987, Wheelwright and Schultz 1994); either mechanism

would yield a positive correlation of age with reproductive success. These hypotheses are clearly not applicable to species that show within-individual increases in reproductive success between successive reproductive bouts (Pyle et al. 1991, Smith 1993).

The second group of hypotheses asserts that older individuals allocate more effort to reproduction. The restraint hypothesis states that this is because residual reproductive value decreases with age, so as individuals become older the value of current reproduction increases relative to the value of future reproduction. This idea is based on the theoretical trade-off between current and future reproduction (Williams 1966, Pianka and Parker 1975) and only applies if the probability of survival decreases with age. Reproductive effort may also increase with age if age-specific improvements in breeding experience make each successive reproductive bout relatively less expensive (Reid 1988). Accordingly, individuals may allocate the same relative effort into reproduction as they age, but increase it in absolute terms. These hypotheses are based on life history, in which age is the explanation.

In contrast, hypotheses in the third group, collectively known as the constraint hypothesis (Curio 1983), are based on ecological considerations. These hypotheses posit that younger individuals are unable to reproduce

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as well as older ones because the former are less capable of competing for breeding opportunities. Age-related variance in reproductive success is considered to be a result of differences in the ability to obtain territories, forage efficiently, resist competitors, avoid predators, attract prospective mates, and/or raise offspring. These factors may, in turn, be affected by the familiarity of individuals with the breeding area. This effect, known as "local experience" or "local familiarity", may allow prior residents to exploit the resources of an area more efficiently than new arrivals (Hinde 1956, Greenwood 1980).

Here we used banding and nesting data from four consecutive breeding seasons to examine the effects of prior residency on several indices of breeding performance in Yellow Warblers (*Dendroica petechia*). The Yellow Warbler is a socially monogamous 10 g passerine found from Alaska and northern Canada to the coasts of Peru and Venezuela, including the Caribbean and Galapagos islands. Formerly, several species, or subspecies were recognized (Aldrich 1942, Bent 1963), but currently these are considered "groups" of one species (Sibley and Monroe 1990). Southern, non-migratory subspecies are easily distinguished from North American migratory populations by morphological differences (Aldrich 1942, Wiedenfeld 1991, Curson et al. 1994) and by phylogenetic analyses based on mitochondrial DNA (Klein and Brown 1994). The migratory group (*Dendroica petechia aestiva*) used in this study, breeds in the United States and Canada and winters in Central America, northern South America, and the Caribbean.

Using morphological and nesting data from four consecutive breeding seasons, we first determined whether prior residence increased the likelihood or timing of breeding in Yellow Warblers. We then tested the survival and dispersal hypotheses by examining whether individuals were more likely to breed or to do so earlier in successive seasons, and we dealt with the possible disappearance of phenotypes from the population by relating morphology and breeding performance to subsequent return rates. Finally, we explored morphological differences between new arrivals and returning birds, and individual morphological changes between successive breeding seasons.

METHODS

Data were collected from 1992 to 1995 at a 5 ha (approximately 500 m × 100 m) area between Pointe à Fourneau and Pointe du Moulin on Île Perrot, Quebec, Canada (45° 22' N, 73° 51' W). Yellow Warblers began arriving to our study area during the second week of May in all four years. Typically one or two males arrived first; two or three days later large numbers of males arrived, along with the first females. Nests are built exclusively by females, and nest-building takes about four days. Eggs are usually laid on consecutive days, at a rate of one per day. Clutches normally contain four or five eggs. Incubation begins when the last egg is laid, and the first egg hatches 10 days later. During the nestling period only females brood, but both parents feed their nestlings. Fledging normally occurs approximately 10 days after hatching.

Adult birds were captured using mist nets; each bird captured was banded with a U.S. Fish and Wildlife Service (USFWS) aluminum band and three colored plastic bands. Mist nets were operated throughout the study area on a daily basis from May to early June, starting at dawn and ending at 11:00–13:00, weather-permitting. Three to five nets were used simultaneously in close proximity to one another, and these were moved such that the entire study area was sampled every 7–10 days. After 3 or 4 such cycles, we focused our effort for 1–2 weeks on unbanded birds whose nests had already been found. Nestlings were banded at the nest when they were six days old, but only with a USFWS band. In any given year, each adult bird captured was classified as a returning bird if it had been banded as an adult in previous years; otherwise it was classified as a new arrival. It is impossible to know with certainty whether every bird was captured every year, so a few returning birds may have been misclassified as being new to the site; all tests must therefore be considered conservative.

Several standard morphological measurements were taken from each bird: the lengths of the flattened wing chord, the ninth primary feather, the outermost rectrix, and the tarsus. The weight of each bird was recorded to the nearest 0.1 g using a calibrated Pesola® spring balance.

From early May to the middle of June the area was thoroughly searched daily for nests, concentrating in areas where birds had been banded and using behavioral cues from females. Except during days of continuous rain, every nest was visited daily to document the chronology of nest building and egg laying. Many nests failed as a result of harsh weather or predators; re-nesting attempts usually followed. Two categorical measures were used to determine the breeding stage reached: whether at least one egg was laid at a given nest (clutch initiation) and whether at least one egg hatched. Clutch initiation and hatching dates were used to indicate the timing of reproduction; replacement nests were not used in these comparisons. Laying date was defined as the date the first egg was laid, and

TABLE 1. Frequency of Yellow Warblers that reached the "first egg" stage depending on whether they were new to the area or returning birds, by year and sex (expected frequencies in parentheses). Heterogeneity tests: males: $\chi^2 = 0.006$, $df = 2$, $P > 0.05$; females: $\chi^2 = 0.706$, $df = 2$, $P > 0.05$.

	n	Did not reach the "first egg" stage		Reached the "first egg" stage		χ^2	P
		New	Return	New	Return		
Males							
1993	47	13 (13.3)	13 (12.7)	11 (10.7)	10 (10.3)	0.02	$\gg 0.05$
1994	71	30 (31.1)	15 (13.9)	19 (17.9)	7 (8.1)	0.09	$\gg 0.05$
1995	53	19 (19.3)	12 (11.7)	14 (13.7)	8 (8.3)	0.01	$\gg 0.05$
Total	171	62 (63.2)	40 (38.8)	44 (42.8)	25 (26.4)	0.06	$\gg 0.05$
Females							
1993	46	21 (16)	2 (7)	11 (16)	12 (7)	8.32	0.004
1994	66	23 (21.1)	8 (9.9)	22 (23.9)	13 (11.1)	0.52	$\gg 0.05$
1995	45	15 (11.4)	4 (7.6)	12 (15.6)	14 (10.4)	3.65	0.056
Total	157	59 (48.3)	14 (24.7)	45 (55.6)	39 (28.3)	11.8	0.001

similarly, hatching date as the date the first egg hatched. As used here, the terms "clutch initiation", "first-egg stage", "laying date", and "hatching date" refer to features of the nest, and therefore apply to both the male and the female associated with the nest. In several other species clutch size often decreases as the breeding season progresses (Erikstad et al. 1985, Murphy 1986, Perrins and McCleery 1989), so only initial nesting attempts were used in comparisons of clutch size. Other estimates of breeding performance were not used in these analyses because intrusive experiments, beginning at the time of hatching but random with respect to the variables examined here, were carried out every year (Lozano and Lemon 1995, 1996, 1998).

Although the date on which birds began to arrive during the four years of the study varied by up to two weeks, the first day on which an egg was laid in the population was fairly consistent. From 1992 to 1995, these first egg dates were May 26 and 24, June 2, and May 25 respectively. These yearly first egg dates were used to account for variation in laying date among years; relative laying and hatching dates of individual nests are defined as the number of days after the respective yearly first egg dates, added to the mean first egg date from all four years.

Relationships between categorical variables were examined using Fisher's exact tests for $n < 20$, χ^2 tests for $40 \geq n > 20$, and χ^2 with Yates' adjustment for continuity for $n > 40$ (Cochran 1954, Fienberg 1980, Everitt 1992). Because the mobility of the two sexes may have differed, especially early in the breeding season when the birds were banded, the data were analyzed separately for males and females. Within-individual increases in size and breeding performance between consecutive seasons were tested with one-tailed paired *t*-tests or Wilcoxon matched-pairs signed ranks tests; if an individual was sampled repeatedly in several years, data from only the first 2 years were used in these analyses. Size differences between groups were also assessed using the four morphological variables in a MANOVA, with group and year as the in-

dependent variables. All statistical analyses were performed or verified using Statistica (5.1 and 98, under Windows 3.11 and 95). Statistical significance was accepted at $P < 0.05$.

RESULTS

Among males there was no relation between prior residence and whether a clutch was initiated in their nests (Table 1). In contrast, among females the number of prior residents that initiated a clutch was higher than expected, as was the number of birds new to the area that failed to initiate a clutch. The pattern was the same in all three years, significant in 2 of the 3 years and in the analysis with data pooled from all years (Table 1). Finally, there were no significant differences in first egg date ($F_{1,151} = 0.65$, $P > 0.05$), clutch size ($F_{1,147} = 0.17$, $P > 0.05$), or hatching date ($F_{1,110} = 0.21$, $P > 0.05$) between birds new to the area and returning individuals.

Differences between groups do not necessarily imply changes within individuals. Comparisons within individuals in successive breeding seasons show no increases in clutch size in either sex (Wilcoxon matched-pairs signed-ranks tests: males $Z = 0.36$, $n = 18$, $P > 0.05$; females $Z = 0.82$, $n = 21$, $P > 0.05$). However, for males laying date was significantly earlier in successive breeding seasons, on average 2.8 days earlier (Wilcoxon matched-pairs signed-ranks test: $Z = 1.78$, $n = 18$, $P = 0.04$; Fig. 1a). This was largely due to late-nesting males nesting markedly earlier in the following year, as there was little difference among males that nested in late

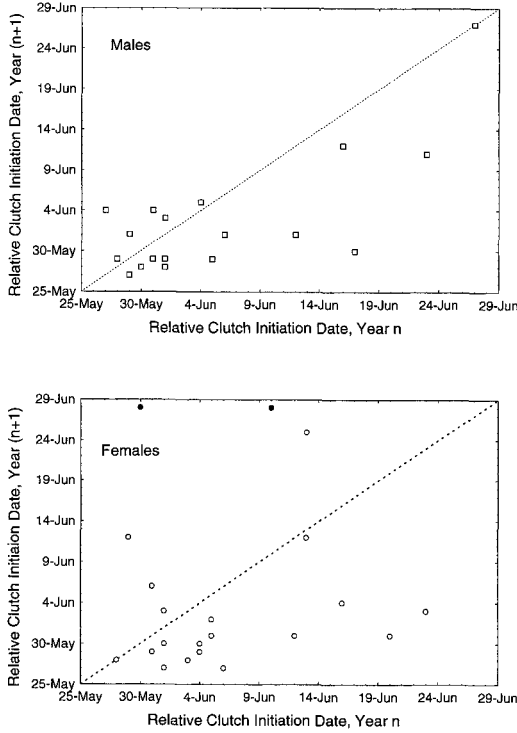


FIG. 1. Clutch initiation dates by individuals in consecutive breeding seasons, corrected for differences between years (see methods). The dashed lines have a slope of 1, which would result if clutch initiation occurred on the same relative date in successive breeding seasons. The two solid circles in the lower graph were categorized as outliers (see results).

May–early June (Fig. 1a). In contrast, the difference in females was only 1.3 days earlier, and was not significant (Wilcoxon matched-pairs signed-ranks test $Z = 0.93$, $n = 21$, $P = 0.18$; Fig. 1b). However, the relationship is heavily influenced by 2 nests that may have been re-nesting attempts. Without these outliers the margin becomes 4.0 days earlier and statistically significant (Wilcoxon matched-pairs signed-ranks test: $Z = 1.85$, $n = 19$, $P = 0.032$; Fig. 1b). The removal of these outliers did not lead to categorically different conclusions in all other analyses.

A significant relationship between breeding performance and subsequent return occurred in only one of the three years. Both males and females that had at least started a clutch in 1992 were more likely to return the following year (Table 2), but there was no evidence of this relationship in the other 2 years. Although the results were also significant when using pooled data, this was due solely to the 1992 results (Heterogeneity χ^2 tests: males $P = 0.014$; females $P = 0.065$; Table 2). Similar results were obtained if return frequency was compared to having hatched at least one offspring. Among birds that nested, there were no significant differences in first egg date ($F_{1,166} = 0.60$, $P > 0.05$), clutch size ($F_{1,166} = 0.21$, $P > 0.05$), or hatching date ($F_{1,137} = 1.10$, $P > 0.05$) between birds that subsequently returned and those that did not. Therefore, the effect of breeding performance on subsequent return, as measured here, was certainly not consistent, if present at all.

TABLE 2. Relationship between having reached the “first egg” stage in one breeding season and returning in the following year. Continuity adjusted χ^2 or Fisher’s exact tests (*) were used depending on the sample size and its distribution (expected frequencies in parentheses). Heterogeneity tests: males: $\chi^2 = 8.51$, $df = 2$, $P = 0.014$; females: $\chi^2 = 5.461$, $df = 2$, $P = 0.065$.

	n	Did not reach the “first egg” stage		Reached the “first egg” stage		χ^2	P
		Did not return	Returned	Did not return	Returned		
Males							
1992	67	29 (20.5)	3 (11.7)	14 (22.5)	21 (12.5)	16.5	<0.001
1993	47	15 (14.9)	11 (11.1)	12 (12.1)	9 (8.9)	0.07	$\gg 0.05$
1994	71	33 (32.3)	12 (12.7)	18 (18.7)	8 (7.3)	0.01	$\gg 0.05$
Total	185	77 (67.4)	26 (35.6)	44 (53.6)	38 (28.4)	8.07	0.005
Females							
1992	37	8 (4.1)	1 (4.9)	9 (12.9)	19 (15.1)	*	0.005
1993	46	17 (14.5)	6 (8.5)	12 (14.5)	11 (8.5)	1.49	$\gg 0.05$
1994	66	25 (26.3)	6 (4.7)	31 (29.7)	4 (5.3)	0.31	$\gg 0.05$
Total	149	50 (43.1)	13 (19.9)	52 (58.9)	34 (27.1)	5.17	0.023

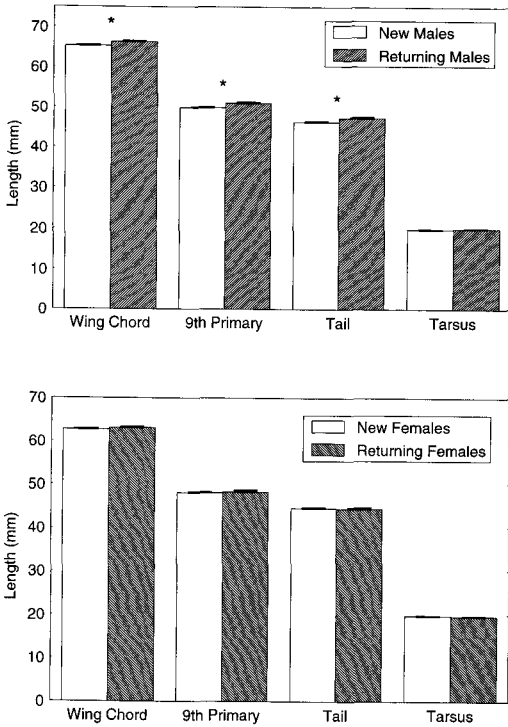


FIG. 2. Mean size (+SE) of Yellow Warblers versus residency history. MANOVAs were carried out using all variables (Males: Wilks' $\lambda = 0.901$, $F_{4,151} = 4.14$, $P = 0.003$; Females: Wilks' $\lambda = 0.976$, $F_{4,133} = 0.803$, $P \gg 0.05$). Asterisks indicate significant differences ($P < 0.05$) resulting from univariate ANOVAs.

Returning males were significantly larger than new arrivals (Wilks' $\lambda = 0.901$, $F_{4,151} = 4.14$, $P = 0.003$; Fig. 2) but returning females were not larger than new arrivals (Wilks' $\lambda = 0.976$, $F_{4,133} = 0.803$, $P > 0.05$; Fig. 2). In

contrast, there were significant within-individual increases in size between successive breeding seasons in both sexes (Table 3).

Finally, there were no significant differences in morphology between nesting birds that subsequently returned and nesting birds that did not return, in either sex (MANOVA: Males Wilks' $\lambda = 0.989$, $F_{4,167} = 0.448$, $P > 0.05$; Females Wilks' $\lambda = 0.9477$, $F_{4,125} = 1.724$, $P > 0.05$).

DISCUSSION

The effects of prior residency on breeding performance differed substantially between the sexes. Comparisons of new arrivals with returning birds showed that the likelihood of breeding increased with prior residency in females, but not in males. Among birds that nested, there were no significant differences in the timing of breeding and clutch size between new arrivals and returning birds. However, within-individual comparisons showed that males began breeding significantly earlier in subsequent breeding seasons. Therefore, the effect of prior residency was greater for females than for males; in females local experience affected the prospect of breeding, and in males it only affected the timing of breeding.

There can be several advantages to breeding earlier. Early breeders often have larger clutches (Erikstad et al. 1985, Murphy 1986, Perrins and McCleery 1989). In the population we studied the median clutch size decreased from five eggs in nests started before June 15, to four eggs in nests initiated thereafter. Fledglings from earlier nests also have

TABLE 3. Within-individual increases in size between successive breeding seasons in Yellow Warblers and results from one-tailed paired *t*-tests.

Variable	<i>n</i>	Difference (mm) Year _{x+1} - Year _x	SE	<i>t</i>	<i>P</i>
Males					
Tail	48	0.50	0.32	1.55	0.06
Wing chord	49	0.46	0.21	2.14	0.02
Ninth primary	49	0.97	0.28	3.53	<0.001
Tarsus	49	0.20	0.14	1.49	0.07
Females					
Tail	31	0.27	0.31	0.89	>0.05
Wing chord	31	0.74	0.34	2.18	0.02
Ninth primary	31	0.74	0.32	2.32	0.01
Tarsus	31	0.31	0.14	2.28	0.02

more time to develop before migration, which in our area begins in the latter half of July. Perhaps most important, nest losses, whether they are due to inclement weather or predation, are very common in open nesting birds (Nice 1957, Martin and Li 1992). An earlier start provides a longer available breeding season, which enhances the probability of re-nesting following nest losses (Lozano et al. 1996).

Birds that arrive first may also benefit by obtaining preferred territories (Wooller and Coulson 1977, Newton 1988, Morris and Lemon 1989, Lemon et al. 1996). On the other hand, early arrivals also risk death from exposure to cold weather and lack of food early in the spring (Anderson 1965, Whitmore et al. 1977). Several other researchers have shown that earlier arrivals are larger and in better condition than later arrivals (e.g., Arvidsson and Neergaard 1991, Lozano 1994, Stolt and Fransson 1995). Size is important because arrival time depends partially on the ability to withstand adverse conditions early in the breeding season. In our population, however, it is unlikely that size affected arrival time, because there was little variance in arrival dates, but even given similar arrival times, large size may still be advantageous in intra-sexual competition during territory establishment and defense (Arcese 1987, Hogstad 1989).

Individual males were larger in subsequent breeding seasons, and, as a group, returning males were also larger than males new to the area. In contrast, returning females were not significantly larger than females new to the area, but individual females recaptured in consecutive breeding seasons were larger from one breeding season to the next. At first glance, the latter results may appear contradictory, but the two analyses are not equivalent. Females may increase in size between consecutive breeding seasons without necessarily leading to returning females being larger than new arrivals. The differences between the sexes may result, for instance, if the breeding dispersal or size variance of females is greater than that of males.

Size may also play a role in mate choice later in the season. In Yellow Warblers extra-pair paternity is widespread (Yezerinac et al. 1995), and within-pair paternity increases

with male size (Yezerinac and Weatherhead 1997). Female preference for larger males may occur if size is an honest indicator of phenotypic or genotypic quality, or if size is being used as an indicator of age. If there is a genetic component of survival ability, age, in itself, would be a measure of genetic quality, and females would benefit by mating with older males (Manning 1985).

We do not know the exact ages of all adult birds studied, but we assume the mean age of new arrivals is less than that of returning birds. This is because in Yellow Warblers breeding dispersal is limited (Yezerinac and Weatherhead 1997), but natal dispersal is common, as it is in birds in general (Greenwood 1980, Greenwood and Harvey 1982, Clarke et al. 1997). We have no measures of dispersal exclusive of mortality, but only 4.5% of all nestlings returned, compared to an overall yearly return of 36% for adults. Although we cannot be certain that every individual classified as a new arrival was only one year old, returning birds were, by necessity, at least two years old. Therefore, when compared as two separate groups, not as individuals, it is safe to conclude that returning birds were older than new arrivals (see also Yezerinac and Weatherhead 1997).

Age-dependent increases in reproductive success have been well documented in birds (reviewed by Sæther 1990, Forslund and Pärt 1995), but the proximate mechanisms responsible have been difficult to determine because potential factors are often correlated. Apparent age-dependent increases in reproductive success can be a statistical consequence of the gradual disappearance of poor breeders from a population, which would result if the phenotypic or genotypic quality of an individual affects both its chances of breeding and surviving (Curio 1983). Alternatively, individuals may be more likely to disperse to other areas in subsequent breeding seasons after a failed breeding attempt (Harvey et al. 1979, Bensch and Hasselquist 1991). Either mechanism would yield a difference in reproductive success between age classes, but this did not occur in our study. Except for one year, breeding performance did not affect subsequent return for either sex. Furthermore, there were no morphological differences between birds that subsequently returned and those that did not.

These results also confirm that non-breeders were not actually transients, captured while on route to their final destinations. Had this been the case they would have been less likely to return than breeders.

The restraint hypothesis proposes that young individuals deliberately withhold reproductive effort. Life-history theory suggests that age of first reproduction is an important component of lifetime reproductive success (Charlesworth 1980, Clutton-Brock 1988). Our records show that 64% of all adult Yellow Warblers fail to return, which makes it very unlikely that individuals would purposely forego the opportunity to reproduce, especially after having already migrated to the breeding grounds. Moreover, the decision not to reproduce would be optimal only if there is a large cost to reproduction, but we found that breeding was not related to subsequent return rates. Therefore, the restraint hypothesis is probably not appropriate to explain age-dependent increases in reproductive success in Yellow Warblers or other short-lived migratory species (Wheelwright and Schultz 1994).

Our results are consistent with the constraint hypothesis, which predicts that younger birds are disadvantaged when competing for breeding opportunities. However, it is difficult to know to what extent these results are caused by differences in local experience or by age in itself. Experimental work will be required to determine the ecological and proximate mechanisms responsible for these differences (Martin 1995).

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