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Experimental evidence of the territorial defense hypothesis in insular Blue Tits

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Abstract. Many insular vertebrates have unusually high population densities and are characterized by behavioural shifts including reduced territory size and reduced situation-specific aggressiveness. Compared to their mainland counterparts, Blue Tits on the island of Corsica exhibit many traits that fit the trends observed in crowded insular populations. We demonstrate from behavioural observations in aviaries and from hormone measurements that Corsican tits are less aggressive than mainland ones. These shifts, as well as changes in reproductive patterns, support the defense hypothesis.

Key words. Blue Tit; defense hypothesis; insularity; aggressiveness; breeding traits; sexual hormones.

In their paper 'The territorial defense hypothesis and the ecology of insular vertebrates' which reviews the literature on island biotas, Stamps and Buechner[1] emphasized that the social behaviour of a variety of insular vertebrates (reptiles, mammals, and birds) reveals a remarkable similarity in behavioural traits: 1) reduced territory size, 2) increased territory overlap, 3) acceptance of subordinates, 4) reduced situation-specific aggressiveness, and 5) abandonment of territorial defense. Two non-exclusive hypotheses have been proposed by these authors to explain these shifts in behavioural traits: 1) The 'resource hypothesis' suggests that territorial behaviour is adjusted to resource densities which are more abundant and less variable on islands than on mainlands; hence abundant food resources, associated with lower competition and predation rates in species-poor islands[2], allow higher population densities of those species that are present. These high population densities result in changes in spacing behaviour and decrease in territory size. 2) The 'defense hypothesis' suggests that the costs of defense against territorial contenders and intruders are higher on islands because of high population densities. Stamps and Buechner argue that these behavioural shifts, and especially a decrease in aggressiveness may occur as a result of exaggerated defense costs in crowded populations. They also suggest that reproductive and growth patterns of insular vs mainland conspecifics reflect elevated defense costs on islands and suggest that many insular vertebrates reallocate their breeding resources so as to produce young that are more competitive. Although it seems difficult to make such generalization for any island biota, an impressive literature (reviews in refs. 1, 2 and 3) emphasizes both the behavioural shifts cited above and many changes in populations, especially unusual high densities, niche enlarging, lower fecundities and the production of a few competitive offspring. Here we examine these hypotheses from data on the comparative biology of Blue Tit *Parus caeruleus* L. between mainland and island habitats and from experiments in aviaries.

Life history of the Blue Tit on the mainland and on the island

Long term population biology studies of the Blue Tit comparing an insular population on the island of Corsica, France, and several populations on the nearby mainland, have shown striking differences in many traits[4-7]: 1) Island Blue Tits have much higher population densities (10.6 breeding pairs per 10 ha vs 4.8, before the erection of nest-boxes). 2) Their territory size is half as large (0.94 ha) in Corsica as on the mainland (2.08 ha) with large territory overlaps. 3) Tits start to lay on average three weeks later. 4) Their breeding commitment is much lower (clutch-size is 6.3 eggs ± SD = 1.1 vs 8.6 ± 1.4). 5) They never have second or repeat broods unlike the mainland population where a proportion varying between 7% and 37% do, depending on the years and habitats. 6) The proportion of yearlings (breeding birds born the previous year) is higher on the island (37% as compared to 23.5% on the mainland). 7) The nestling period is slightly longer on the island (22 days instead of 18–19 days) in spite of their being a smaller number of nestlings. 8) Contrary to theoretical predictions on the evolution of life-history traits on islands[2,3], breeding adults do not survive better on the islands (adult survivorship = 56%) than on the mainland (57.5%), but yearling survival probability is very high on Corsica (65%)[7]. 9) Parents bring a larger diversity of prey to their nestlings—in particular fewer caterpillars, a prey which is always preferred whenever available[6,8] (a large diversity of prey of unequal quality is a good indication of food shortage[6]).

Most of these results (i.e. 1–7) fit the trends cited in the introduction but two (8, 9) do not. First, the fact that adults do not survive better on the island than on the mainland runs counter to a well-established dogma[7]. On the other hand, a higher survival of fledglings relative to that of adults in Corsica is consistent with the resource reallocation hypothesis and may be related to a parent-offspring conflict for survival[9]. The second factor that does not fit the generalization on island biotas refers to food resources, an essential environmental component which is not measured in most studies on island vertebrates. Zandt et al.[10] have shown that the food supply, especially caterpillars which are a key food resource for tits, is far less abundant and is available much later in the season in Corsica than on the mainland. This is explained by the patterns of foliage renewal of evergreen oaks which are the dominant tree species in Corsica, whereas the trees where tits forage on the mainland are deciduous. In contrast to deciduous trees which renew their whole foliage each spring, no more than 30% of the leaves of evergreen trees are renewed each year[11]. Therefore, only one third of the leaves of evergreen trees are edible by folivorous arthropods such as caterpillars because leaves more than a few months old are much too hard and contain chemical repellents such as tannins. The patterns of resource abundance for insectivorous birds on Corsica also runs counter to a dogma of more abundant resources in equitable and benign insular climates. Thus the resource hypothesis is certainly not the best one for explaining the behavioural shifts in Blue Tits on Corsica. However, Corsican tits do exhibit a lessened aggressiveness as demonstrated below.

Methods and results

In an experiment designed to test the hypothesis of a strong genetical component in laying date[5], two samples of 12 Blue Tit nestlings, one from a continental population (Mont-Ventoux, southern France) and the second from Corsica, were hand-raised. The birds from the two regions were raised in a third region (Montpellier) in 3 m × 3 m × 3 m aviaries where food availability and environment were standardized. This design reduced environmental imprinting and maternal effects and left the genetical component of laying date to be expressed. The test showed that captive birds of both regions started to breed in all three years of the study at almost exactly the same date as that of the wild populations they came from[5].

A second aim of this experiment was to compare the aggressiveness of the birds, and more specifically, to test the predictions of the defense hypothesis[1] that island birds are less aggressive, a test which has not been performed before. During the first three years of the experiment (1986–1988) we paired each bird with a partner from the same region (table 1). Pairing these sexually monomorphic birds had been successfully achieved using the ratio of oestrogenous/androgenous hormones from the faeces[12,13]. This ratio gives a measure of the sexual activity of the birds. The behaviour of the birds of the two regions, especially courtship patterns and the process of pair formation were normal, so that they bred successfully for three consecutive years (1986–1988, Mainland Males × Mainland Females and Island Males × Island Females, denoted as MM, MF, IM and IF respectively, see table 1). In 1989 we cross-paired the birds and made two crosses of an island male (IM) with a mainland female (MF) and four crosses with a mainland male (MM) and an island female (IF). Samples were admittedly small (because of the cost of such experiments) but the experiment was designed so that the same birds were utilized for within-

Table 1. Top: Laying date (LD, 26/4 = 26 April) and clutch-size (CS) of pairs of Blue Tits with within-region (mainland/mainland, island/island) and between-region (mainland/island) partners, Ident. = ring numbers (IF522 = Island female No. 522). Bottom: Laying date ± 1SD and Clutch-size ± 1SD of the Blue Tit in the wild populations. Range in brackets

Aviaries	Mainland Males				Island Males			
	Year	Ident.	LD	CS	Year	Ident.	LD	CS
Mainland Females	1986	MF522 × MM348	26/4	9				
	1987	MF522 × MM350	22/4	5				
	1988	MF522 × MM505	22/4	5	1989	MF522 × IM814	4/5	6
	1987	MF524 × MM570	26/4	5				
	1988	MF524 × MM570	23/4	5	1989	MF524 × IM474	2/5	5
Island Females	1988	IF802 × MM350	1/5	10*	1986	IF401 × IM474	10/5	7
	1989	IF401 × MM570	Failure		1987	IF401 × IM474	8/5	8
	1989	IF478 × MM479	Failure		1988	IF401 × IM474	28/4	11
	1989	IF488 × MM505	3/5	6	1987	IF488 × IM792	11/5	6
					1988	IF488 × IM796	10/5	7
					1988	IF478 × IM788	24/5	5
Wild populations								
Mainland (1986–1989, N = 74)			26/4 ± 5.14 (13/4–7/5)	8.6 ± 1.39 (5–12)				
Corsica (1986–89, N = 194)							9/5 ± 5.87 (25/4–26/5)	6.7 ± 1.08 (4–10)

*eggs were unfertilized

and between-region pairing, avoiding biases due to inter-individual variation in behavioural and breeding traits.

Results (table 1) show that in the two experiments where island males have been paired with mainland females (IM × MF) the males influenced laying date since the two mainland females (MF522 and MF524) laid later than when they were paired with a mainland partner in 1986–1988 (3 May vs 24 April on average, table 1). This laying date was slightly earlier than the average laying date of the wild Corsican population (9 May, N = 194) but fell within the range of variation of first clutch laying date (table 1). The problem is to know whether this male influence is genetic or behavioural. Since van Noordwijk et al.[14] have shown for the Great Tit *Parus major* L. that most of the genetic component of laying date is due to the female, we conclude that the influence is mostly behavioural. These two Corsican males were not aggressive and exhibited a late and very weak courtship behaviour. Moreover, they hardly assisted the females in building the nest and feeding during the period of egg laying and incubation. Such weak courtship displays of the males presumably explain the delay of laying date of these mainland females.

In the opposite situation, where mainland males have been paired with island females, four cases gave the following results: 1) The female IF802 paired with MM350 laid on the 1st of May, a date that is later than the mean laying date on the mainland but earlier than the mean laying date of the wild population on Corsica, although it nevertheless falls within the range of laying dates on this island (table 1). The behaviour of the male did not significantly affect the timing of laying. But this male which had successfully bred in 1987 with MF522 was extremely aggressive, and the Corsican female always escaped from his attempts to copulate with her so that the three clutches she laid were unfertilized. 2) MM570, which successfully reproduced in 1987 and 1988 with MF524, was very aggressive and continuously chased the female in the aviary. This female, which successfully bred in 1986–1988 with IM474, was only able to bring a few pieces of nesting material into the nest-box. 3) MM479, paired with IF478, hunted her down continuously so that the pair did not even attempt to breed. 4) Finally, MM505 was paired with IF488. These two birds successfully bred in previous years with partners of the same region, MM505 with F522 in 1988 and IF488 with IM792 in 1987 and IM796 in 1988. The male (MM505) was dominated by other MM when they were put together in a same aviary after having been hand-raised in August 1985, so that we had to isolate it. In the 1989 cross-pairing experiment, IF488 laid on 3 May instead of 11 May in both 1987 and 1988. She laid only 8 days earlier with her MM partner than with her former IM partner and produced a clutch of 6 eggs. The nest was deserted soon after clutch completion.

In summary, the two mixed IM × MF pairs were successful in building a nest and producing fertilized eggs but the males exhibited weak and late courtship behaviour, which presumably explains the delay in egg laying. On the other hand, of the four cross-region experiments with MM paired with IF, one pair produced unfertilized eggs, two pairs failed in their breeding attempt and in the fourth the female deserted the eggs. In these four crosses, the males were so aggressive that they repelled rather than attracted their mates. In the four cases where females laid eggs, the laying date was slightly later than the region-specific date for the mainland females and slightly earlier for the island females (table 1).

A physiological indication of differences in aggressiveness between mainland and island males is given by the ratio of sexual hormones in the faeces of the birds. The oestrogenous/androgenous hormone ratio (O/A), which depends on the gonadic activity, is responsible for the behaviour which assists the breeding process. It is usually smaller than 1 for males and higher than 1 for females[13]. For males, the smaller the ratio the larger the sexual activity, because androgens mediate display behaviour and increase social status and aggressiveness which is the first response of the male in pair formation[15,16]. The O/A ratio depends on the sexual activity of the birds in the course of the year, but comparisons can be made provided that measurements are taken at the same period of the year. We measured these ratios in December 1985, for both mainland and island birds, which were still juvenile at this time. Since testosterone induces both aggressiveness and singing activity[16,17], and since these traits correlate with testosterone levels throughout the year in both adults and juvenile males[18], one would predict that the lower the O/A ratio, the higher the level of aggressiveness. Our measurements fit these predictions since O/A ratio was significantly (one tailed U-test, $p < 0.05$) lower in mainland males ($O/A = 0.29 \pm SD\ 0.24$) than in island males ($O/A = 0.86 \pm SD\ 0.50$, table 2). The low O/A ratio in mainland males as compared to that in island males presumably explains the exaggerated sexual-aggressive behaviour of the former and the chasing component of the display which did not change from aggressiveness to courtship. One cannot rule out, however, the possibility that the differences are because of captivity biases, but such biases are unlikely since all the birds have been raised in the same experimental conditions.

Discussion

This experiment shows that Corsican males are much less aggressive than mainland males. One problem is that differences in breeding time between island and mainland birds could result in a physiological mismatch

Table 2. Oestrogenous/androgenous hormone ratios (O/A) of mainland and island captive Blue Tits. Symbols are identification numbers (MM570 = mainland male No. 570)

	Mainland	O/A	Island	O/A	p
Males					
	MM570	0.12	IM402	0.87	
	MM515	-	IM474	0.20	
	MM523	0.34	IM476	1.02	
	MM571	0.74	IM486	1.37	
	MM505	0.16			
	MM350	0.09			
	MM348	0.30			
	MM397	-			
Mean:		0.29 ± 0.24		0.86 ± 0.50	<0.05
Females					
	MF522	2.70	IF401	3.92	
	MF524	3.52	IF478	2.58	
	MF521	1.57	IF488	3.71	
			IF484	4.35	
			IF486	4.35	
Mean:		2.59 ± 0.97		3.77 ± 0.76	NS

of hormones. This could explain for instance why the Corsican females refused to copulate with their mainland mates and why the latter chased the females and became more aggressive. Such a mismatch is probably not the underlying cause of the pattern, however, because it does not explain why the differences in aggressiveness between island and mainland birds remained unchanged all the year round in the aviaries. Moreover, we have two additional indications of lower aggressiveness in island males. First, at the beginning of the experiment, the hand-raised 'fledglings' (which were born in May 1985 on the mainland and June 1985 on Corsica) were put together in two aviaries, one for the mainland birds and the other for the Corsican birds, in August 1985. A very strong aggressiveness among MM, with feather losses on the forehead because of injury from competitors, soon forced us to separate them, whereas not a single case of harmful aggressiveness has been noticed among Corsican males, which kept together for several months (until January 1986). Second, ten extra full grown birds caught in Corsica in November 1986 (6 males and 4 females) did not manifest any aggressiveness for the two weeks they spent together in the same aviary. Circumstantial observations in the wild populations suggest a very weak territorial defense in island males: in contrast to mainland birds, males respond very weakly to playbacks of males' song (playback experiments were carried out with region-specific songs).

The reduced aggressiveness of birds in crowded insular populations runs counter to the trend usually observed in mainland populations where increased densities often result in increased situation-specific aggression[19]. However, a decrease in aggressiveness among high-density insular vertebrates is so widespread[1] that it must contain a strong fitness component. This behaviour is closely related to the 'stranger-neighbour' effect, whereby discrimination between neighbours and strangers minimizes the energy expended in aggressiveness and prevents escalated contests between neighbours[20]. Increases in defense costs predict a reduced source gain for territory holders, and reduced rates of resource accumulation predict reduced biomass production (e.g. reproductive output). Defense costs of Blue Tits on Corsica are assumed to be high because of severe food constraints in a habitat with high population densities and strong competition for territory. Blondel et al.[21] interpreted these high densities by density compensation mechanisms in species-poor islands. In such crowded situations, birds have to increase the time spent foraging and/or enlarge their territories in order to gather the extra energy required for defense. Abandonment of territorial defense under strong intrusion pressure has been observed in a number of species[1]. When defense time reaches a threshold beyond which the bird cannot support its maintenance and defense requirements, it is expected to abandon defense of the territory[1,22]. Contrary to theoretical predictions[22], birds have not been observed to increase their territory size as a response to a decrease in resource abundance. Instead they show shifts in a variety of traits including behaviour, a decrease in brood size, shortened breeding season, and a single brood per season[7]. Such patterns support the defense hypothesis which predicts lower rates of biomass production per territory owner in overcompensating faunas[21]. This is exactly the pattern found on Corsica. In such circumstances, saving time and energy by reducing defense costs and decreasing territory size should be selected for, because this behaviour improves fitness payoffs per territory owner for those individuals that exhibit such behavioural shifts. Thus, the later start of breeding on Corsica, smaller clutch-size, absence of second broods, reallocation of resources (including longer parental care[7]) producing few competitive offspring, and the diversified and water-poor[6] diet of the nestlings are all consistent with the hypothesis that food limitation is the underlying cause of the reduced aggressiveness of insular Blue Tits.

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