



sex, which did not necessarily include coitus, lowered primary immune responses (Krees et al., 1989; Ostrowski et al., 1989). In pied flycatchers (*Ficedula hypoleuca*), females given an immune challenge decreased the amount of maternal care (Ilmonen et al., 2000). In house sparrows (*Passer domesticus*), an immune challenge generally led to decreased feeding rates (Bonneaud et al., 2003). Therefore, there is increasing evidence that activities such as courting, mating and offspring-rearing can have detrimental effects on immunocompetence and vice versa. Our current challenge is to understand under what circumstances responses are, or are not, detected.

One approach is to manipulate the independent variable (e.g., brood size) and then observe the effects on immune function. An unmanipulated animal is expected to allocate available resources to all required functions optimally, neither neglecting nor devoting undue resources to any one system, whereas, in the manipulated system, a negative correlation is expected: in the unmanipulated situation the same energetic trade-offs predict a positive correlation between immune function and other condition indices (Lochmiller and Deerenberg, 2000). Even in such unmanipulated situations, immunocompetence is expected to differ between classes of animals (e.g., sexes or ages) because of differences in physiology (e.g., sex hormones — Schuurs and Verheul, 1990; stress hormones — Sapolsky, 1992) or, at the ultimate level, life history (Folstad and Karter, 1992).

Noting that testosterone causes the development of secondary sexual traits in most male vertebrates, and that it also depresses immune function, Folstad and Karter (1992) proposed the 'immunocompetence handicap hypothesis', which argues that individual males face a testosterone-mediated trade-off between the allocation of resources to secondary sexual traits and immune function (Tause4f)2(

that birds that had initiated development of ornamental feathers earlier would be in better condition (e.g., Piersma and Jukema, 1993). We also predicted that immunocompetence would be positively correlated with the degree of development of these testosterone-induced characters. Finally, it has been suggested that the morphs have somewhat different life histories, with independents being more successful per breeding bout, but satellites starting to breed at younger ages and/or living longer (Widemo, 1998). If satellites live longer than independents, one would expect them to invest more on self-maintenance; therefore, we also tested whether satellites had stronger immune responses than independents.

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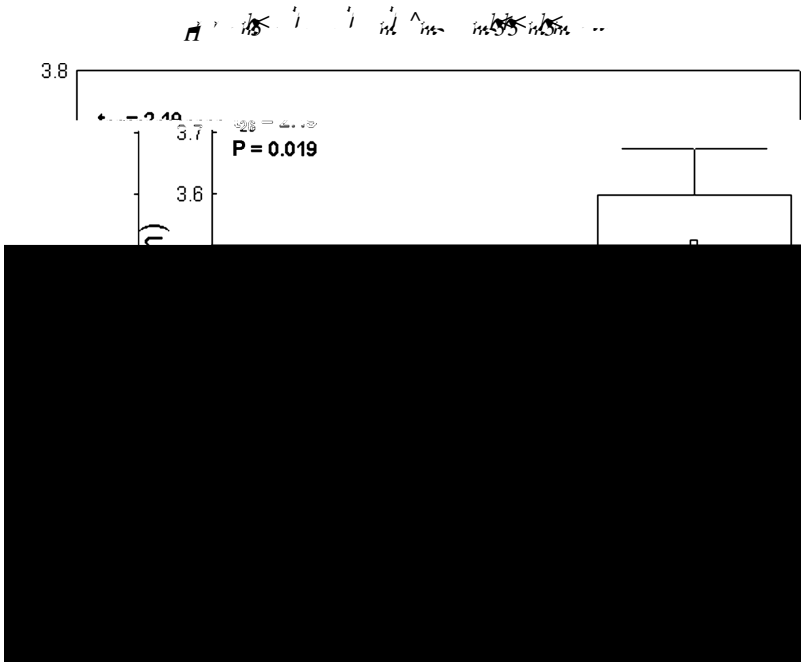
Parry, 1974; Klasing, 1988; Deerenberg et al., 1997) and a subcutaneous delayed hypersensitivity response (Glick, 1986; Corner and DeLoach, 1990; Roitt et al., 1996) to assess humoral and cell-mediated acquired immunity, respectively. The SRBC hemagglutination assay entails exposing the animal to SRBC and quantifying the resulting production of SRBC-antibodies. The delayed hypersensitivity test consists of an injection of a mitogen that causes T-lymphocytes to mobilise to and

relationships expected among measures of conditions in this observational study. All analyses followed the standard tests for homoscedasticity and homogeneity of variance when appropriate. Statistical significance was accepted at  $\alpha < 0.05$ .

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Tarsus length did not differ significantly between the two morphs, but independents had longer culmens (35.9 vs. 35.1 mm,  $t_{26} = 1.94$ , one-tailed  $\alpha = 0.03$ ) and were more massive (182.7 vs. 168.3 g,  $t_{26} = 2.29$ , one-tailed  $\alpha = 0.015$ ) than satellites.

Independents were more massive than satellites even when accounting for body size, either by means of an ANCOVA with tarsus as the covariate (Morph  $_{[1,25]} = 4.92$ , one-tailed  $\alpha = 0.018$ , Tarsus  $_{[1,25]} = 0.42$ , one-tailed  $\alpha = 0.74$ , interaction



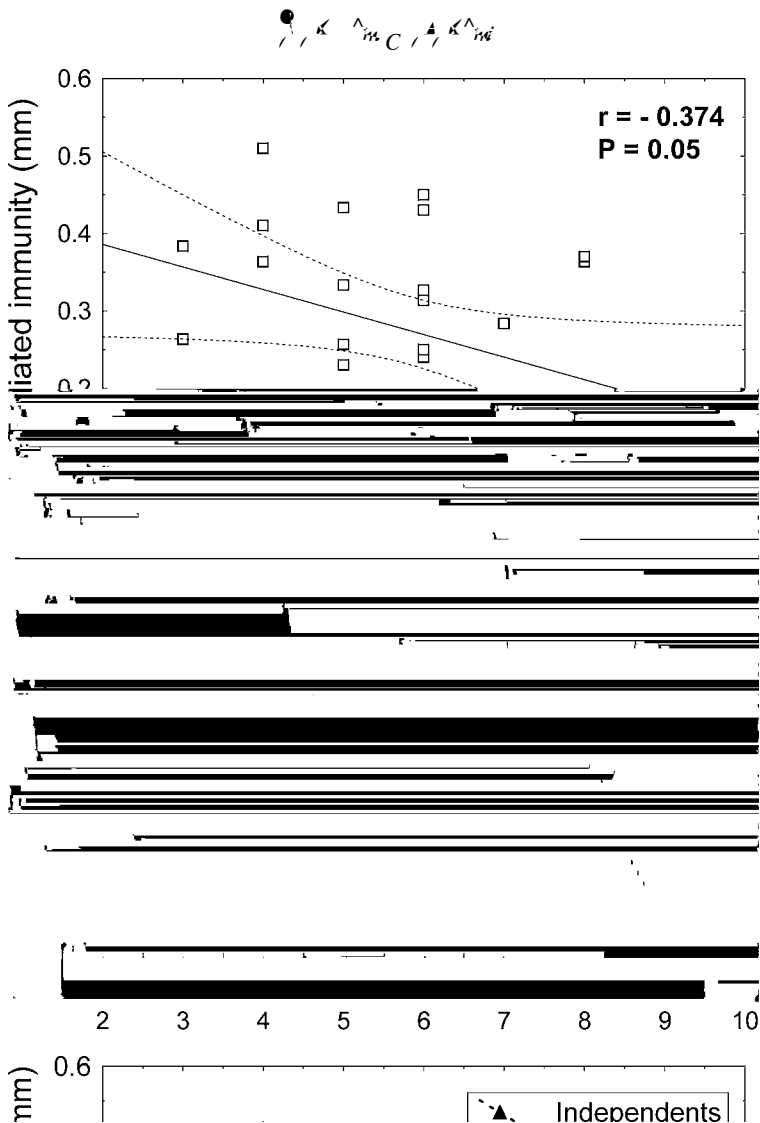
Differences in condition (mass/size) between independents and satellites. Box plots indicate the mean, s.e., and 1.96 s.e.

Correlations of size (PC1), mass/tarsus, ruff length, wattle number, and two measures of immunocompetence in male ruffs (n = 28). CMI = cell-mediated immunity. Each cell includes the respective Pearson correlation coefficient and associated P-value, two-tailed for correlations involving size, one-tailed for all others (see text). Asterisks indicate statistical significance. Parentheses indicate significance using sequential Bonferroni.

	Mass/tarsus	Ruff <sup>^</sup>	Wattles	SRBC	CMI
Size (PC1)	-0.300	0.429	0.549	0.346	0.028
	0.121	0.025	(0.002)	0.057	0.886
Mass/tarsus		0.029	-0.036	0.1264	0.055
		0.442	0.573	0.261	0.39
Ruff <sup>^</sup>			0.568	0.049	0.346
			(0.001)	0.405	0.038
Wattles				0.107	0.122
				0.294	0.268
SRBC					-0.160
					0.209

<sup>^</sup> n = 27, one outlier excluded.

wattle number nor ruff length was significantly correlated with mass/tarsus, but they covaried positively with each other and were also positively correlated with body size (table 1).



Decrease in cell-mediated immunity, measured in mm of response to PHA injection (see text), with age in male ruffs. Upper: all birds included,  $n = 28$ , linear regression and 95% C.I. Lower: Separately for resident and satellite morphs (ANCOVA: morph  $_{[1,25]} = 6.03$ ,  $\Upsilon = 0.021$ ; age  $_{[1,25]} = 7.5$ ,  $\Upsilon = 0.011$ ; morph-age interaction NS).

Cell-mediated immunity was not significantly correlated with size, mass/tarsus, or wattle number, but was weakly related to ruff length (table 1). There was a decrease in cell-mediated immunity with increasing age (fig. 3;  $r = -0.37$ ,  $n = 28$ ,  $\Upsilon = 0.05$ ), which was still present, but not quite significant, when morphs were analysed separately (independents:  $r = -0.43$ ,  $n = 19$ ,  $\Upsilon = 0.06$ ; satellites:  $r = -0.61$ ,  $n = 9$ ,  $\Upsilon = 0.081$ ). With age as a covariate, satellites did not have



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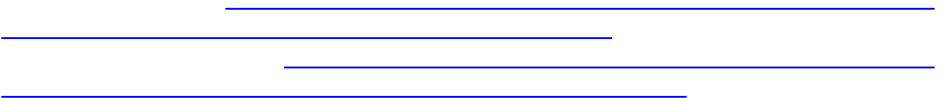
$$\hat{\beta}_{C_i} = \frac{\sum_{j=1}^n C_{ij} Y_j}{\sum_{j=1}^n C_{ij}^2}$$

agreement (Ewenson et al., 2001) with previous work. Cell-mediated immunity increased with ruff length, and the relationship between humoral immunity and body size was suggestive, but not significant (table 1). Taken together, these results indicate that at least early in the breeding season, different parts of the

highlight the need to measure several parts of the immune system and perhaps have several indices for each.

The concept of trade-offs, central to life-history theory, is based on the assumption of energetic or resource constraints. Ad libitum food probably dampens the magnitude and variability of these trade-offs relative to what might occur in the wild (Hoi-Leitner et al., 2001; Alonso-Alvarez and Tella, 2001; Ewenson et al., 2001). Hence, whereas positive correlations between the extent of plumage development and similar measures of body condition were documented in a related species in the wild (Piersma and Jukema, 1993), ad libitum food might explain why these correlations were not significant in our study. Despite captive conditions, however, males maintained substantial variability in the timing and extent of development of plumage and wattle traits, and mass, including a difference in 'condition' between morphs parallel to that seen in the wild (Bachman and Widemo, 1999). While it could be argued that trade-offs should not exist when food is not limited, studies continue to demonstrate otherwise (e.g., Bilbo et al., 2002; Casto et al., 2002; Cuthill et al., 1997; Prendergast and Nelson, 2001). Trade-offs come in many forms: metabolic, physiological, social, genetic, phylogenetic, and whereas ad libitum food might understandably shift the equilibrium, it does not remove all costs. In our case, males were housed communally, engaged in extensive social interactions, and began to develop their seasonal sexual traits at different times and to different maximum extents. The concept of trade-offs, central to life-history theory, is actually based on the assumption of adaptations to energetic or resource constraints; adaptations that do not necessarily cease to exist once the constraints are removed.

The stable genetic polymorphism of ruffs requires mean per capita lifetime reproductive success to be equal in the long run. Widemo (1998) observed that independents obtained a higher per capita and per annum proportion of matings at leks, and suggested, as one possibility, that the morphs have different life-history strategies. Satellites, which do not defend territories, may adopt a lower cost, lower annual benefit strategy involving breeding at a younger age and/or



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