Avian behaviour

Altruism and infidelity among warblers

In cooperatively breeding vertebrates, indirect fitness benefits[1,2] are maximized by subordinates who choose to help their own closely related kin after accurately assessing their relatedness to the group's offspring[3–5]. Here we show that in the cooperatively breeding Seychelles warbler (*Acrocephalus sechellensis*), female subordinates help to raise new nestlings by providing them with food only when the offspring are being raised by parents who also fed the subordinates themselves when they were young[3]. These helper females use the continued presence of the primary female, rather than of the primary male, as their provisioning cue — presumably because female infidelity is rife in this species[6], making their relatedness to the father less reliable.

In *A. sechellensis*, female offspring normally become subordinate within their natal group[7,8] and often help to raise dependent young[7]. We studied the provisioning behaviour (feeds given per hour) of 21 colour-ringed female subordinates. Reproductive sharing and high levels of extra-pair paternity occur in this species[6]; we therefore assessed parentage and genetic relatedness by using microsatellite DNA markers[8]. Subordinate parents (that is, subordinates who had also produced a nestling in the helped nest) always provisioned and were excluded from subsequent analysis ($n=8$).

In a general linear model analysis, the provisioning behaviour of non-parent subordinates was influenced positively by subordinate–nestling relatedness ($F_{1,11}=4.82$, $P=0.05$, $R^2=0.31$), whereas subordinate age, sex, number of nestlings, number of subordinates (or feeding adults) and territory quality had no significant effect. A comparison of relatedness[9] to the nestlings of subordinates who helped with those that did not (Fig. 1a) indicates that helpers were significantly related to nestling(s), whereas non-helpers were not (mean relatedness, 0.27 versus −0.05, respectively).

The continued presence of the primary female, but not of the primary male, was a reliable cue of subordinate–nestling relatedness; subordinate–primary female relatedness predicted subordinate–nestling relatedness ($F_{1,38}=27.37$, $P<0.001$), but subordinate–primary male relatedness did not ($F_{2,37}=2.11$, $P=0.16$). Subordinates provisioned significantly more often when their putative mother was still present, but provisioning was unaffected by the presence or absence of the putative father (Fig. 1b).

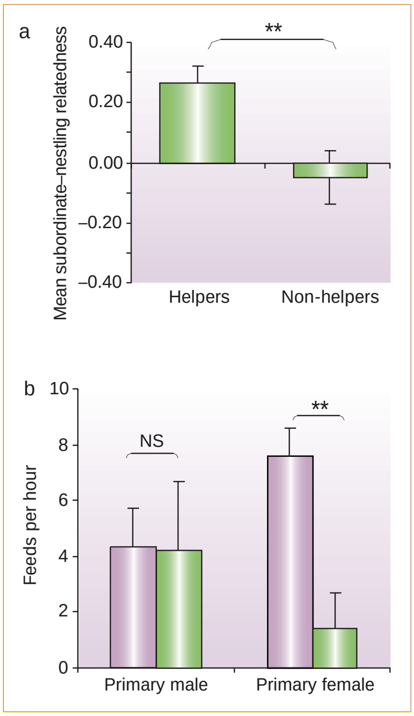

Figure 1 Provisioning by subordinate female, non-parent Seychelles warblers (*Acrocephalus sechellensis*). **a,** Provisioning in relation to the pairwise relatedness between subordinates and nestlings (subordinate helper–nestling relatedness versus non-related: 0.27 ± 0.16 versus 0, one-sample *t*-test, $t_7=4.64$, $P<0.002$; helpers versus non-helpers: 0.27 ± 0.16, $n=8$ versus −0.05 ± 0.20, $n=5$; $t_{11}=3.13$, $P=0.01$). **b,** Provisioning in relation to the presence (purple bars) or absence (green bars) of the subordinate's putative parents (presence versus absence of putative mother: 7.57 ± 2.44, $n=6$ versus 1.43 ± 3.60, $n=7$; *t*-test, $t_{11}=3.71$, $P=0.003$; presence versus absence of putative father: 4.30 ± 4.89, $n=4$ versus 4.24 ± 4.29, $n=8$; $t_{11}=0.02$, $P=0.98$). Error bars, means ± s.e.; asterisks indicate statistical significance.

Subordinates may determine when to provision by directly assessing their relatedness to either the nestling(s) or the primary female. However, the continued presence of the primary female explained provisioning more reliably ($F_{1,11}=13.72$, $P=0.003$, $R^2=0.55$) than genetic estimates of subordinate–nestling or subordinate–primary female relatedness ($F_{1,11}=2.14$, $P=0.17$; $F_{1,11}=0.06$, $P=0.81$, respectively). These results confirm that the presence of the primary female who raised the subordinate is likely to be used as a cue to determine when to provision. Previous findings that helpers can distinguish between siblings and half-siblings[3] may have been an artefact caused by helpers assisting only their mothers.

Our results show that female subordinates can use an indirect but reliable cue to assess their relatedness to nestlings, and that this assessment of kinship determines provisioning rates. In *A. sechellensis*, the amount of food brought to the nestling determines fledging success and first-year survival, and the presence of a helper increases the number of young who are fledged on a territory[10]. The preferential provisioning of related nestlings by female subordinates will therefore increase the number of related offspring produced. In our study, the number of fledglings produced on a territory increased significantly (by 17%) for each subordinate present (after exclusion of direct parentage)[8].

Both direct[8] and indirect benefits may be important within this cooperative breeding system as, by using effective discrimination, subordinates are able to maximize the indirect benefit gained within a system that is driven primarily by direct benefits[8]. Our findings show that, in the presence of a high frequency of female infidelity, an associative learning mechanism has evolved to focus on the mother at the nest — the only sex to which the subordinates are reliably related.

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COMMUNICATIONS ARISING

Plant ecology

Tree-species competition and coexistence

How apparently similar plant species coexist is a puzzle. Kelly and Bowler[1] claim that environmental fluctuation promotes the coexistence of tree species by alternately favouring recruitment of common and rare congeners in a dry tropical forest. Here I argue that current knowledge of tropical-forest ecology does not support the authors' focus on congeneric competition, and show that their use of diameter distributions to date recruitment fluctuations may be misleading. It is therefore doubtful, at this stage, that recruitment patterns of the authors' congeneric pairs can be linked to the sort of competition dynamic that they envisage.

Kelly and Bowler's two-component lottery model assumes that seedlings of congeners compete for the same set of establishment sites, the availability of which is little affected by other taxa. Empirical evidence from other tropical forests suggests, however, that this is unlikely. Although it is reasonable to assume that closely related taxa have similar requirements, most tropical trees seem to have broad, overlapping niches[2–4] and so are likely to compete for establishment sites with a wide variety of taxa, and not just with close relatives. There is little reason, therefore, to argue that a 'see-saw' model of interaction between congeneric pairs, discounting diffuse competition, is an informative approach to the dynamics of a forest containing more than 200 tree species.

Kelly and Bowler present evidence of out-of-phase recruitment fluctuations in rare and common congenerics. Recruitment fluctuations were inferred from proxy age distributions, dividing trunk diameters by species-specific mean recent growth rates to estimate individual trees' ages. A problem with this procedure stems from the assumption that diameter distributions are a reliable indicator of age distributions. The fragility of this assumption is well known to dendro-ecologists working in temperate forests[5–8], where growth-ring counts allow ages to be estimated accurately. The often-poor correspondence between diameter distribution and age structure[5–9] probably arises because stand dynamics have subjected different age classes to different growth histories, as well as spreading a given age class across a wide range of diameters.

The implications for Kelly and Bowler's method are exemplified by data from a temperate forest[9] showing that 'recruitment fluctuations' inferred from diameter distributions and age–diameter relationships do not necessarily coincide with those suggested by the actual age data (Fig. 1). Therefore, although tree-diameter distributions can reasonably be used to draw broad inferences about age structure (such as distinguishing between all-aged and even-aged populations), attempting to date recruitment fluctuations by such a method is probably overly ambitious[5–7].

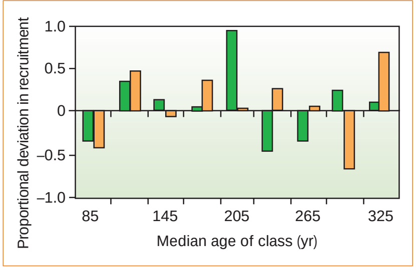

Figure 1 Recruitment fluctuations as indicated by population age structure (green bars) and by use of stem diameter as a proxy for age (orange bars) in a population of *Weinmannia racemosa* ($n = 216$) in an old-growth temperate forest in New Zealand[9]. Fluctuations are represented as proportional deviations (observed − expected/expected) from a negative exponential curve[1]. Despite the highly significant overall relationship between age and diameter ($r = 0.81$, $P < 0.0001$), there is no correlation between 'real' and proxy fluctuations ($r = 0.03$, $P = 0.94$).

In view of the difficulties of reliably dating recruitment fluctuations, and the questionable basis of the model, the case for mediation of coexistence of congeners by environmental fluctuation is unconvincing. Although there is every reason to believe that environmental instability contributes to coexistence in general[10], establishing even the potential for its special relevance to the regeneration of congeneric trees in tropical forests would require clear evidence that seedlings of coexisting congeners overlap far more in space and time than they do with those of more distantly related associates.

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Plant ecology

Coexistence of tropical tree species

For decades, ecologists have struggled to explain how so many tropical tree species can coexist. Kelly and Bowler[1] propose that differences in recruitment fluctuation and competitive abilities among closely related tree species could promote coexistence, and data from a tropical deciduous forest in western Mexico seem to confirm their predictions. We argue, however, that the tests of their model's predictions make fundamentally flawed assumptions about both size–age relationships in trees and the factors that influence population size structures. As such, their results are potentially misleading and lack the necessary rigour to "reject all other theories of coexistence".

Kelly and Bowler's model of species coexistence predicts that rare species should exhibit greater deviation in recruitment than common species. To test this, they compared differences between expected and observed age-class distributions for ecologically similar congeners. In essence, they predicted that abundant species should show fewer deviations in historical recruitment trends, and thus have 'smoother' age-class distributions.

Determining the age of tropical trees is challenging because most such species do not form annual growth rings[2]. Kelly and Bowler circumvent this problem by using average diameter-growth rates to convert tree size to age (that is, age = size/growth rate). This, however, makes the improbable assumption that average lifetime growth rates are the same for every tree in a species' population. Evidence from both temperate and tropical forests contradicts this assumption[3,4]. Tree growth is indeterminate, and in natural forests the availability

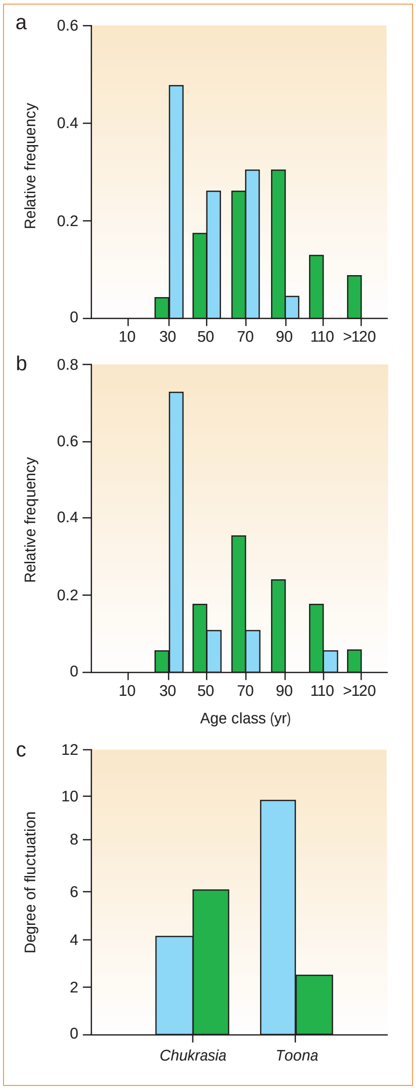

Figure 1 Comparisons of real (blue bars) and size-derived (green bars) age distributions for two tropical tree species that form annual growth rings. **a,** *Chukrasia tabularis*; **b,** *Toona ciliata*. **c,** Degree-of-fluctuation (*d*) values for real and size-derived age distributions. Data were obtained from canopy trees in a 50-hectare, permanent forest-dynamics plot at the Huai Kha Khaeng wildlife sanctuary, western Thailand. Real age distributions were obtained from tree-ring analysis. Estimated tree ages were calculated from cored trees by dividing stem diameter by a taxon-specific mean annual growth rate. Note that the estimated age distributions differ in both shape and scale from the real age distributions and that the values of *d* for the estimated distributions provide no indication of *d* for the real age distributions.