CEES

annual report 2010

Animal Ecology

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Group leader   Prof. dr. Theunis Piersma

Composition of the group in 2010:

Tenured Staff	source	fte	period
Dr M.W. Dietz	RUG	0.6	
Prof. dr. Ir. J. Komdeur	RUG	1.0	
Prof. dr. T. Piersma	RUG	0.7	
Dr. B.I. Tieleman	Rosalind Franklin Fellowship	1.0	
Prof. dr. J.M. Tinbergen	RUG	1.0	
Post-docs			
Dr. C. Both	NWO-VIDI	1.0	070101-120101
Dr. H.L. Dugdale	NWO-Rubicon	1.0	091101-101130
Dr. I.K. Lesna	PVE	0.3	080218-100815
Dr. K.D. Matson	NWO-VENI	1.0	081001-110930
Dr. J.W.H. Reneerkens	NWO-ALW	1.0	070201-100430
PhD Students			
Drs. C. Burger	RUG-FWN	1.0	080501-120430
Drs. J. van de Crommenacker	WOTRO	1.0	060101-100101
Drs. E.O. Folmer	RUG Breedtestr.3	0.8	031201-081201
Drs. S. Grizard	RUG/FWN	1.0	100101-131231
Drs. M. Hammers	NWO/ALW	1.0	081001-120930
Drs. A. Hegemann	Vogelbescherming-FWN	1.0	060301-101130
Drs. M. Hinsch	NWO-VICI	1.0	040901-080901
Drs. N.P.C. Horrocks	NWO-VENI/FWN	1.0	060401-100401
Drs. B. de Jong	IWT / RUG FWN	1.0	100101-121231
Drs. R. Kentie	LNV / RUG FWN	1.0	071216-111215
Drs. M. Langenhof	RUG-Ubbo Emmius	0.9	091201-140630
Drs. J. Leyrer	MAVA-NIOZ	1.0	050801-090801
Drs. T. Lok	ALW NWO	1.0	080301-120228
Drs. P.M.G. Lourenço	Portuguese Sci Foundation	1.0	060101-100101
Drs. S.P.M. Michler	NWO-VICI	1.0	040401-080401
Drs. J. Ouwehand	NOW/ALW	0.8	100513-150201
Drs. H. Ndithia	Nuffic	1.0	100601-140531
Drs. R. Radersma	NWO-VICI	1.0	070416-110415
Drs. L. Schmaltz	RUG-Prov. Friesland	1.0	091001-130930
Drs. J. Schroeder	RUG	1.0	040315-080715
Drs. E. Schut	RUG FWN	1.0	060901-100901
Drs. C. Trierweiler	St.Werkgr. Grauwe Kiekendief	1.0	050601-090601
Drs. O.H. Vedder	EC-FWN	1.0	061201-101201
Drs. Y.I. Verkuil	RUG	0.8	040315-090616
Drs. M.A. Versteegh	NWO-VENI/FWN	1.0	060401-100731
Drs. J. van der Woude	NWO-VICI	1.0	081001-120930

Fitness consequences of helping in the cooperatively breeding Seychelles warbler

Hannah Dugdale, David Richardson, Jan Komdeur & Terry Burke

Cooperative breeding is observed in birds, mammals, fish and insects. It is a social system in which group members care for offspring that are not their own. Individuals are selected to maximise their fitness, so why do some individuals help others to breed, rather than focusing on their own reproduction? Charles Darwin considered this apparently altruistic act to be one of the most important tests of evolution by natural selection. Kin selection theory later formulated how altruistic behaviour may evolve by natural selection; however, measuring fitness (the relative contribution of a genotype to the next generation) in natural systems remains problematic. One of the major questions in evolutionary biology is, therefore: why has cooperative breeding evolved?

Without cooperative breeding, competition for the limited breeding habitat will result in smaller territories and a pool of non-breeding individuals. Cooperative breeding may be the 'best of a bad job' – allowing otherwise unproductive individuals to gain a small fitness benefit by helping to raise at least some additional relatives. Conversely, it may represent an alternative and equally productive life-history strategy if the fitness benefit of helping equals that of an unhelped breeder on a suboptimal territory. Comparing these alternative scenarios requires an understanding of how they affect lifetime reproductive success, in terms of the number of offspring raised in each generation. Furthermore, the recognition that helping has fitness benefits has led to the assumption that individual variation in helping is a plastic response to different environments. For cooperative breeding to evolve, however, there must be selection favouring helping, and helping must be heritable. It is vital to investigate the heritability of helping and its fitness consequences in order to gain a complete understanding of how and why cooperative breeding has evolved.

Figure 15. (A) a Seychelles warbler chick being fed at the nest (courtesy of Jildou van der Woude), and (B) the genetic pedigree of 1,057 warblers, split into six generations (the top-line is the first generation) with lines going from mothers (red) and fathers (blue) to offspring. Grey lines represent 544 birds that did not have helping data.
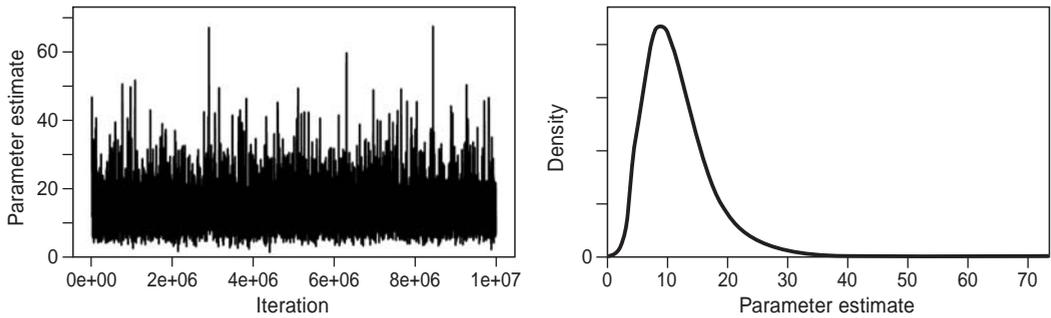
Figure 16. Markov Chain time-series (left) of 9,950 estimates of individual variation in helping. The posterior density (right) does not overlap zero, demonstrating individual variation in helping.

These questions have previously been intractable because they require powerful genetic markers (to accurately assign parentage), a closed natural population that is fully monitored (to accurately record survival, fecundity and life-history decisions) and long-term data (to monitor these parameters over complete lifetimes). The Seychelles warbler is a facultative cooperative breeder and is ideally suited for this purpose (Fig. 15A). This is because 30 microsatellite markers facilitate accurate parentage assignment (Fig. 15B) and there is virtually no immigration or emigration of Seychelles warblers between islands, enabling accurate measurement of both survival and fecundity. From 1997 onwards, nearly all of the warblers on Cousin Island have been individually colour-ringed, and their status (helper, non-helper, dominant) identified in each breeding season until death. It is therefore possible to follow the decisions of individuals over their lifetimes and to relate these to the realised fitness benefits. This is rare; hence, it offers one of the few cases where major evolutionary questions can be unravelled in a natural population.

Using Bayesian methods, we built a genetic pedigree of 1,057 warblers, of which 75 were and 438 were never observed helping. Warblers exhibited individual variation in helping behaviour (Fig. 16). Contrary to analy-sis of earlier years (1986–1995), the probability of helping was not sex biased, but it did show annual variation (1997–2006). A power analysis suggested that the pedigree had power of 0.8 to detect heritabilities greater than 0.24, but this did not enable separation of the individual variation into an additive genetic component.

Complete lifetime data were available for 209 warblers. Individuals that helped in their lifetime had greater lifetime fitness than those that did not, using both lifetime reproductive success (the number of chicks that a bird was assigned parentage of in its lifetime; $W = 6007$, $p < 0.001$) or individual fitness (λ, $U = 5579$, $p = 0.02$, Fig. 17A). De-lifed fitness (pt(i)) revealed that this was due to increased fecundity ($U = 5219$, $p = 0.04$), rather than increased survival ($U = 4909$, $p = 0.26$; Fig. 17B).

We therefore demonstrate selection for helping behaviour, and individual variation in this trait, which is a pre-requisite to heritability. A further 500 genotypes will be added to the pedigree. This will significantly and disproportionately increase the pedigree's power by increasing the mean depth to at least three generations. The current mean pedigree-depth is two generations; thus, adding 500 individuals will effectively double our power – a conservative analysis suggests that it will
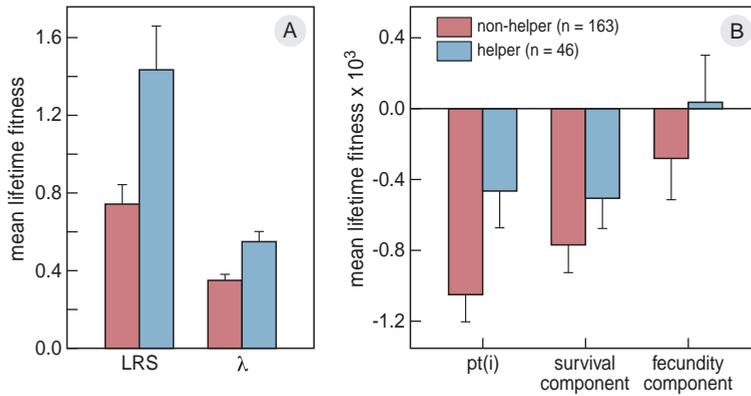
Figure 17. Mean lifetime fitness of Seychelles warblers that were observed helping or not-helping in their lifetime, where fitness was measured as A) lifetime reproductive success [LRS] and individual fitness [λ], and B) de-lifed fitness [pt(i)]. Error bars display the standard errors (S.E.); n = number of warblers.

provide power of 0.8 to detect heritabilities of at least 0.16.

Behavioural traits impact upon the fitness of individuals. Understanding the strength of selection on behaviour and the genetic and environmental components of these is vital for a complete understanding of evolutionary processes. Our findings improve our understanding of the adaptive basis of reproductive decisions in the cooperatively breeding Seychelles warbler, providing wider insight into the evolution of cooperative breeding.

Infection, immunity, and island-life

Kevin D. Matson, Sophie Vergouwen, Nicholas P.C. Horrocks & B. Irene Tieleman

Immune systems evolve in response to pathogens. Because of their isolation, oceanic islands are thought to have low pathogen pressures; therefore, island inhabitants might exhibit reduced immune function. In fact, some insular animals do exhibit increased disease susceptibility, and some insular populations declined spectacularly following pathogen introductions. To investigate how infectious threats shape immune systems, we study birds in the continental USA (Ohio) and on Bermuda, an isolated oceanic island. we quantify immunological and fitness (e.g., nestling growth, survival) parameters in the presence and absence of experimental treat-ments designed to alleviate disease pressure. We also collaborate with others on a parallel study investigating the infectious threats faced by eggs and the corresponding level of maternal investment in eggs and egg defenses. Overall, these integrative studies are designed to provide insight into how microbes, diseases, and avian immunological subsystems interact and vary across different locations and scales.

Islands, such as the Galápagos, are often seen as natural laboratories for studying evolution. One isolated island group that has received relatively little attention in terms of the evolution and ecology of its terrestrial