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Dingemanse N.J. 2003. Natural selection and avian personality in a fluctuating environment. PhD thesis, Faculty of Biology, Utrecht University. ISBN: 90-6464877-8, 119 pages,

This thesis is about animal personality. Specifically, the personality of one bird species, the Great Tit *Parus major*. It focuses on the fitness consequences of exploratory behaviour, forming a pivotal part of a larger Netherlands Institute of Ecology program researching this personality trait. The thesis addresses several of the most pressing problems in animal personality research: what does animal personality mean, how can it be measured, and why is it important? Research on the evolutionary ecology of personality traits has languished somewhat in the doldrums, with relatively few studies addressing this topic. This is perhaps because previous personality research has often focused on humans or on domesticated and laboratory animals, because 'serious' scientists have steered clear of a concept they view (unfairly) as rather anthropomorphic, or because it is simply an important idea whose time has finally come.

Personality (or temperament) embodies the idea that individual behavioural differences are consistent, to a greater or lesser extent, over time and across situations. Thus we may observe that individuals differ consistently in how exploratory they are – that is, certain individuals are always more exploratory than others – and that these differences cannot be accounted for by state-dependent variables such as hunger level. If this is the case, we could usefully label animals as 'exploratory, or 'unexploratory'. To measure exploratory behaviour, Dingemanse and co-workers presented tits with a novel-environment test: wild birds were brought into the laboratory for a day and released into a room containing 5 artificial trees resembling hat-stands. The total number of flights and hops made within 2 minutes was used as an index of exploratory behaviour: the test is relatively simple and very quick, yet has considerable predictive power.

We already knew that hand-reared tits showed consistent exploratory behaviour, and artificial selection experiments have shown this temperament trait is heritable (Drent *et al.* 2003 and references therein). Moreover, a correlated suite of behavioural traits exist in these birds: exploration of novel environments, of novel objects, and responses to novel conspecifics all correlate. Importantly, novelty is key in this suite of correlated exploratory responses: as Dingemanse describes, if individuals are given the same test repeatedly, so it becomes less novel, variation between individuals vanishes (Verbeek 1998).

What does the work contained in this thesis add to this story? Demonstrating consistency is

vital to show the personality trait actually exists, and to examine personality structure. Demonstrating heritability has obvious evolutionary implications, and begs the question of how the genetic variability underlying exploratory behaviour is maintained. Dingemanse and co-workers bring natural selection to the story, examining the exploratory behaviour and fitness of wild birds. The project initially aimed, ambitiously, to introduce eggs from selection lines into a natural population. This approach failed, resulting in a change of tack. (Incidentally, it would be interesting to know why this approach went wrong!). Instead, the researchers performed the massive undertaking of measuring exploratory behaviour in 1342 wild tits over 4 years, simultaneously measuring several components of fitness: survival, offspring production, offspring dispersal, and offspring recruitment into the breeding population.

Now, to the specifics. Some of the most significant findings are already published. For example, Dingemanse *et al.* (2002, experimental chapter 1), demonstrated that exploratory behaviour in Great Tits is repeatable (by examining recaptured individuals) and heritable (by parent-offspring and sibling analyses). However, neither body weight at testing nor age predicted exploratory behaviour, though other studies have found that such variables can influence exploration (Greenberg 2003). Experimental chapter 2 examined winter dominance rank at feeding tables, finding that dominance is not a measure of personality, but instead seems to depend on an individuals personality, state, and environment. Experimental chapter 3 (Dingemanse *et al.* 2003) details how natal dispersal (the distance moved between the birth location and that of first breeding) correlated with parental and individual exploratory behaviour in 3 data sets: fast-exploring parents had offspring that dispersed furthest, immigrants were faster explorers than locally born birds, and the distance between birth nest box and feeding station at capture (a correlate of dispersal distance) was larger for fast-exploring females than slow-exploring females. Dingemanse et al. suggest that differences in exploratory behaviour are the cause and not the consequence of dispersal behaviour, since differences in exploratory behaviour arise before dispersal. However, it will always be difficult to firmly assign the cause to exploration alone in such cases, considering that exploratory behaviour correlates with a number of other traits.

Given that the majority of the above findings are published and so will be familiar to many readers, perhaps the final part of the thesis is the most interesting, examining exploration, breeding performance and offspring recruitment. Nest success, fledgling size and condition were all related to the exploratory behaviour of the breeding pair, whereas laying date and clutch size were not. Fledglings in the best condition came from assortative pairs (fast-fast or slow-slow explorers), though, oddly, disassortative mating was observed in older birds. In one year, one with a good beech crop, assortatively mated pairs produced most offspring surviving to breeding, which fits with the fledging condition finding. However, in two years with poorer winter food supplies, intermediate-exploring parents produced most recruits, suggesting that fledging condition cannot entirely determine survivorship. Thus disassortative mating may be advantageous in such conditions, if the likely results are offspring of average exploration speed. We must be cautious in assigning the across-year differences to the differences in the beech crop, but what is clear is that selection on a personality trait fluctuates across years, suggesting a possible mechanism for the maintenance of genetic variation underlying this trait.

In summary, Dingemanse's thesis forms a significant part of an impressive body of work on Great Tit personalities that makes a compelling case for personality research being an important topic. Rather than discussing and speculating on the possible implications of personality for fitness, the researchers have actually gone out and measured them in a massive field study. The results are important to ecology, evolutionary biology, and to anyone interested in the behaviour of birds in the wild.

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Van Gils J.A. 2004. Foraging decisions in a digestively constrained long-distance migrant, the Red Knot (*Calidris canutus*). PhD thesis, University of Groningen, Groningen, The Netherlands Copies can be optained through j.vangils @nioo.knaw.nl

It is fairly rare to see the integration of multiple fields of research within one scientific study. It is equally rare to find ecologists studying a system at various levels of organization, from the cell to the whole animal or from the individual animal to the population. However, there is at least one exception to this informal rule: Jan van Gils, in his thesis on foraging decisions in Red Knots, has put together an impressive amount of data, integrating information from organ to population level.

This thesis is about how the molluscivorous Red Knot *Calidris canutus*, a shorebird species that prominently feeds on low quality bivalves (containing 80-90% of indigestible shell matter), adjusts its foraging decisions to the variable ecological conditions of its environment. As demonstrated in the nine papers that form the body of the thesis, foraging decisions must incorporate many variables (energy requirements, diet composition, food patch quality and availability, presence of conspecifics, predation risk, etc) and, most of all, these animals are digestively constrained by the size of their gizzards, the organ responsible for the crushing and processing of shell material in the food. The knot's gizzard is the key to Van Gils' work.

Van Gils gathered a large group of collaborators (17 co-authors), and a small army of volunteers to run an elegant series of experiments both in controlled and field conditions. The main approach was to apply existing foraging models, updated for the digestive limitation, to the concepts under study in order to generate predictions on foraging decisions in knots. Then, using data collected in specifically designed experiments with captive birds, the predictions could be tested and the findings then used to explain patterns observed in the field. Van Gils' work challenged many previously published foraging models. Indeed, typical foraging models are based on prey handling time as the main limitation on energy intake rate and work in cases when prey are abundant. However, as already pointed out by previous authors, most animals are constrained by digestion rather than by handling. This is especially true for the knot because of the inherent nature of its food which is swallowed whole and contains a lot of shell 'ballast' material that needs to be processed for the animal to meet its daily energy requirements. As clearly demonstrated in the thesis, Red Knots can actually handle their bivalve prey much faster than they can process them in their gizzard, with the result that they fill-up that section of the stomach very fast. Because the muscular gizzard can't keep up with the rate of prey intake, the birds have to take digestive pauses to "make room" for more food. By doing so, rather than by slowing down when feeding, these birds maximize long-term net energy intake rate. They choose their prey type based on digestive quality (energy/shell mass) instead of profitability (energy/handling time), a fact well demonstrated by Van Gils for birds under both captive and wild conditions.