The potentials of personality for reintroductions

Kurt Kotrschal

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There is increasing evidence that individuals in vertebrate populations vary in a non-random way in their disposition to respond to environmental stimuli along an axis between "proactive" and "reactive" (KOOLHAAS et al. 1999). Personalities develop between genes and stimuli; of particular importance are early maternal hormones and post-hatch/birth social environment. "Proactive" individuals are more aggressive and quicker to respond to novel stimuli than "reactives". "Proactives" actively cope with challenges, they are prone to form routines and are quick, but superficial explorers. In reverse, the more dedicated "reactives" are more likely than the "proactives" to innovate. Within populations, individual coping styles are usually continuous and normally distributed. Testing (behaviour and stress hormone reactivity) can reveal individual coping style (personality) early after hatching/birth. Hence, founder populations can be assembled in a way to maximize individual survival and individuals can be specifically trained before release (e.g. proactives to be wary of certain novel stimuli). Thereby, the recent progress in ethological personality research may take some guesswork out of creative conservation management.

K. K., Konrad Lorenz Forschungsstelle für Ethologie, A-4645 Grünau 11, klf.gruenau@telecom.at

Introduction

With the exception of conceptual trivia, such as the monitoring of spatio-temporal activities, behavioural biology and its central concepts had only a minor role in conservation management (CLEMMONS & BUCHHOLTZ 1997, GOSLING & SUTHERLAND 2000). However, more often than non, threatened populations vanish despite of habitat protection; reintroductions always demand immense effort at an only vague chance of success. However, where outcome-orientated ecology may be at its limits, process-orientated ethology may still provide answers.

Even though preservation of primary habitats must remain the highest priority in conservation management, this is often not possible. The ideology of "the natural", fending nature from human influence is increasingly doomed to fail in our dynamically changing world. The same is true for the "genetic determinist" mentality, relying on (i.e. in reintroductions) the appropriate subspecies/genotype, but neglecting the importance of ontogenetic processes for preparing individuals for their new environment.

Imprinting, and different other mechanisms of social and individual learning have already been used to prepare animals for coping with specific challenges of their environment (HÖLZER et al. 1995). However, ethology has more to offer to conservation biology. For example, individuals within species/populations vary in a rather predictable way in how they cope lifelong with environmental and social challenges (KOOLHAAS et al. 1999). Not only humans show "personality" (described by attributes such as introvert-extrovert) or "temperament" (the emotional side of personality), a similar individual differentiation was found in mice, rats, tits, geese, gulls, quail, etc. Aside of genetic factors, maternal steroid hormones and early (social) stimuli shape these stable individual behavioural dispositions. In the following, I will provide a short overview over personality patterns and mechanisms, emphasizing the effect of maternal testosterone in the yolk of geese and quail and will discuss the potentials of these mechanisms for conservation management.

Methods

Following a literature review of patterns found in a variety of species - I will summarize our work in Grünau. This includes testing for coping styles in Greylag geese (*Anser anser*) and Japanese quail (*Coturnix coturnix japonica*) from

hatching to fledging. Individuals were tested in open field, with novelty, detour for food or social contact, exploration and learning tasks, tonic immobility and monitoring the social performance. In a number of experimental animals, behavioural phenotypes were shifted from "reactive" to "proactive" (KOOLHAAS et al. 1999) by injecting testosterone (geese: 300 ng, quail: 50 ng in sesame oil) into the fertilized eggs before incubation (SCHWABL 1993).

Performance of greylag goslings in a series of lerning tasks will be used to link personality with mechanisms of social learning, which finally leads to the establishing of adaptive social traditions in colonizing groups. The evident potentials of such mechanisms for founder populations will be considered.

Results

Patterns

Studies in a range of vertebrates, from fish to man, have shown that individuals in populations vary predictably in how they approach novelty (fast to slow), which is contingent with a suite of other behavioural dispositions (table 1) as well as with physiological parameters to cope with stressors and hence, with energy management (KOOLHAAS et al. 1999). To a considerable extent, "individual variation" in behaviour is not random. Hence, simple screening may allow to select optimally suited individuals for certain tasks. Knowing the mechanisms leading to the expression of individual personalities/coping styles would even allow to "produce" optimally suited individuals on demand.

What causes personality differences?

Human twin studies as well as selection experiments in blue tits (DRENT & MARCHETTI 1999) and mice (BENUS et al. 1989) indicate a considerable heritability of personality attributes (genetic contribution to variability usually 0.3-0.5). Hence, animals can be selected and bread for adequate personality (for example to generate optimal behavioural phenotypes for farm environments). But also environmental stimuli during ontogeny have decisive roles.

Among the most determining stimuli are early steroid hormones (diffusing in utero between siblings or from the mother to the foetus, or deposited in egg yolk). It was shown, for example, that yolk testosterone contents in canaries correlate positively with begging vigor of the chicks and also with their propensity to become dominant later in life (SCHWABL 1993). Similar effects have been shown for a number of birds and mammals and even fish. Hence, it seems that this is a common, phylogenetically highly preserved mechanism in vertebrates.

After hatching/birth social stimuli may also affect the maturation of personality. It was already shown in the 1950ies, that early disturbance of the mother-offspring relationship in social species such as rhesus monkeys and greylag geese lead to attachment disorders (BOWLBY and many others, see FISCHER-MAMBLONA 2000) producing uncertain, aggressive, etc. individuals. I will not presently expand on this aspect.

"Phenotypic engineering": producing and testing personalities

Whether or not the correlation between yolk testosterone contents and personality (see above) is causal, can be tested by experimentally enhancing yolk testosterone. This should result in hatchlings, whose personality is shifted towards "proactive". Hence, we injected testosterone in amounts just to boost, but not to exceed the physiological range (in higher concentrations, testosterone is a developmental toxin) into fertilized, non-incubated eggs of greylag geese and Japanese quail. This indeed resulted in the expected behaviour changes (J. DAISLEY & K. KOTRSCHAL unpubl.). Hatchlings from treated eggs were moving more actively and quicker to approach novel objects than control individuals, they were quicker and more focused in a series of learning experiments and excreted less corticosterone metabolites following episodes of social stress. All these results indicate that early testosterone is indeed a powerful modulator of personality.

Personality and individual roles in a social group

Another line of evidence indicates that personality may indeed predispose individuals for a certain performance in a social group (PFEFFER et al. 2002). Of 13 greylag goslings, 8 learned to open lids of food containers at the age of 6 weeks after hatching and excreted significantly

higher amounts of corticosterone thereafter than the 5 individuals attempting, but unable to solve the task. Out of this group of 8, four at an age of 10 months post hatching, but none of the others learned to pull a string to operate a food dispenser. Again, the performers excreted significantly higher amounts of corticosterone, than the controls. Already days after hatching, control samples revealed that the corticosterone excretion of the 8/4 performers at the first and second task, respectively, was already significantly higher than of the later non-performers. This indicates that the would-be innovators/producers are predisposed by a certain personality/emotionality. High corticosterone reactivity is indicative of a personality being rather "reactive" (table 1) and attentative towards environmental stimuli.

Hence, with such a background of knowledge, individuals of founder populations can either be selected according to local requirements and may be subject to pre-release training specific for their personality (see below).

Discussion

A range of personalities in natural populations

In existing populations a range of personalities may efficiently balance environmental variability. In stable environments, for example, proactive individuals may be of advantage because of their propensity to form routines. In reverse, reactive individuals may be better off in variable environments. Actually, groups with a balanced composition may do best at some stochastic environmental variation (e.g. due to weather or unpredictable resources/predators). A range of personalities in the same group may, via behavioural partitioning of how resources are used even enhance the carrying capacity (Drent & Marchetti 1999) of the environment.

If it would be advantageous to be either proactive or reactive, disruptive selection would quickly create a bimodal distribution of phenotypes. However, this was not shown till now for any natural population. To the contrary, personalities seem to be distributed in a broadly bell-shaped way in most populations, indicating that

Table 1: Contingent behavioural traits and physiological stress responsiveness in “proactive” and “reactive” copers (Terminology according to Koolhaas et al. 1999). Based on Benus et al. (1989), Drent & Marchetti (1999), Wilson et al. (1994) and others. - *Verhaltensmerkmale und physiologische Stressreaktionen bei “proaktiven” und “reaktiven” Individuen (Terminologie nach Koolhaas et al. 1999). Nach Benus et al. (1989), Drent & Marchetti (1999), Wilson et al. (1994) u.a.*

proactive	behavioural trait	reactive
high	aggressiveness, competitiveness	low
bold	response to predators	shy
fast	approach of novel objects	slow
high	locomotory activity	low
far	stray from group, dispersal	close
high	contingency with becoming dominant	low
low	social attachment	high
high	"social independence"	low
fast/superficial	style of exploration/foraging	slow/dedicated
fast/superficial	learning, detour, operational tasks	slow/dedicated
yes	routine formation	less expressed
less likely	becoming innovator/producer	more likely
strong	fast physiological stress response (heart beat, adrenaline)	less pronounced
less pronounced	slow physiological stress response (glucocorticoids)	strong

most individuals are found at intermediary ranges and that there is a continuum between the extreme proactives and reactives. As mentioned above, this may be advantageous at the population level. At the level of the individuum, it also provides a means for mothers/parents to adjust the behavioural phenotype of offspring via mechanisms discussed above. This adjustment to environmental and social variability (frequency-dependent strategies/selection) would counterbalance genetic fixation, because selection pressures and hence, the direction of selection would change between successive generations.

Personality and social traditions

When establishing a novel population (i.e in the course of a re-introduction) or when supporting a dwindling population by adding individuals, success or failure may crucially depend on chosing suitable personalities. This was largely left to chance until now. As a rule, initial losses are high. This is explained by the fact that founder populations lack vital individual experience and adaptive group traditions. Hence, most of these initial losses may be accounted for as the costs of these necessary learning processes. To a certain extent, such costs are unavoidable, however, the price to be payed may be minimized by choosing a well-informed approach.

The two groups of semitame, free-ranging birds introduced for research purposes in the Almtal, greylag geese (introduced 1973) and waldrapp ibis (introduced 1997), may serve as examples. In both cases, individuals received some implicit training by being hand-reared (e.g. spatial bonds developed via social bonds, hence, inhibiting initial dispersal). But personality was given no consideration. In the geese, postfledge-mortality during the two initial years (1973/74) was 60 %, dropping to considerably below 10 % in the following years. In the ibis, we lost 24 of 30 birds (80 %) to predators and to dispersal in the first two years (1997/98), but not a single bird thereafter. Including the first two offspring fledged from this group in 2001, 24 birds are now roaming our valley. Testing for personality and specific pre-release training may have reduced these high initial losses, which could have been fatal, when only a very limited number of precious founder individuals would have been available, as is often the case in reintroduction projects.

When re-introducing captive-bread swift foxes it was indeed shown, that reactive individuals had a higher initial survival than proactives, probably because the latter were not shy enough and easily fell victim to cars and natural predators (BREMNER & ELWOOD 2001). This again stresses the necessity for pre-release training, specific for personalities.

Potentials of our present knowledge of personalities

It is clear today, that individual variation in behavioural phenotype is not random, but follows rules. Individual behavioural phenotype can be influenced by selective breeding, by early steroid exposure and by early experience and the behaviour of coping types in certain situations is predictable. Because coping styles can be identified by early screening, groups can be assembled according to need.

But what does that mean? Under which conditions is it beneficial to be proactive or reactive or intermediate? As discussed above, this may depend on the frequency distribution of coping types in a population and on environmental variability. Founder populations may do better, if reactives preveil, because of the higher tendency of the latter to maintain social cohesion. Also, reactives will be more tolerant and less aggressive towards group members than proactives and they will be more cautious in novel environments and hence, will be less likely than proactives to fall victim to predators, as the swift fox example shows (BREMNER & ELWOOD 2001).

A balanced group composition may generally optimise group performance (ecologically and with respect to reproduction: HESSING et al. 1994). In stable, but potentially challenging, competitive environments, proactives will do better, because they tend to be more aggressive and tend to form routines. In variable environments, however, reactives may do better because they remain more flexible and generally more responsive to environmental stimuli than proactives.

Reintroduction projects may have to deal with secondary or altered habitats. There, reactives may have an advantage because of their capa-

city to solve problems. They may be better innovators than proactives and because of their tolerance towards conspecifics may be better models for the social transmission of information (PFEFFER et al. 2002) and hence, may increase the speed of forming adaptive traditions, which actually may tip the balance of a project towards success.

Particularly in cases, where only a limited number of precious individuals for release is available, scanning for personalities has considerable potentials, because it allows to specifically prepare individuals for release and hence, considerably enhance their chances of survival. Proactive individuals, for example should be trained to avoid potential human-related dangers and predators. Also, the decision concerning the release site could be affected by personalities. Whereas it would be advisable to release proactives in remote areas, reactives may do just as well closer to human civilization. Aside of these few examples there will be many more applications for these new ethological results in creative conservation and wildlife management.

Zusammenfassung - Persönlichkeit und Wiederansiedlung

Neuere Erkenntnisse der Ethologie zu den Mustern, Mechanismen und Funktionen der Persönlichkeit erhöhen Vorhersagbarkeit und Beeinflussbarkeit individuellen Verhaltens. Es zeigt sich immer deutlicher, dass bei allen Wirbeltieren (tatsächlich von Meisen bis Menschen) Individuen in Populationen entlang der Hauptachse "proaktiv"-"reaktiv" (Terminologie nach KOOLHAAS et al. 1999[1]; bei anderen Autoren auch "aggressiv-nichtaggressiv", "forsch-scheu", "schnell-langsam" ...) variieren. Persönlichkeit entsteht in der Ontogenie zwischen Genen, vorgeburtlichen mütterlichen Einflüssen (etwa über Steroidhormone) und nachgeburtlichem sozialen Umfeld; sie bestimmt, wie Individuen lebenslang in ihrem Verhalten und bezüglich hormonalem Stressmanagement auf Herausforderungen reagieren. "Proaktive" sind aggressiver, rascher als "Reaktive", weniger scheu ihrer Umwelt gegenüber, auch im sozialen Bereich. "Proaktive" neigen zur Bildung von Routinen und zur raschen, aber eher oberflächlichen Exploration ihrer Umgebung, etwa bei der Nahrungssuche, während die langsameren aber genaueren "Reaktiven" eher zu Innovatoren werden. Die beiden Persönlichkeitsstile sind in Populationen gewöhnlich kontinuierlich und normal verteilt. Tatsächlich scheint diese Mischung auf Populationsniveau von Vorteil zu sein, etwa in der Nutzung von Ressourcen und in der gruppeninternen Kooperation. Persönlichkeit lässt sich bereits früh durch einfache Tests feststellen. Dies erlaubt beispielsweise, Gründerpopulationen (etwa bei Wiederansiedlungen) so zusammen zu setzen und spezifisch nach Persönlichkeit so zu trainieren, dass damit in dem zur Verfügung stehenden Habitat die individuelle Überlebenswahrscheinlichkeit maximiert wird. Somit sind diese neueren ethologischen Erkenntnisse geeignet "Blindflugstrecken" im kreativen Artenschutz erheblich zu verringern.

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[1] Diese Terminologie bezieht sich auf aktive oder passive Bewältigungsstrategien. So wurden Ratten mit einem schwach elektrisch geladenen Metallgegenstand konfrontiert, von dem sie beim Erkunden einen schwachen Stromschlag erhielten. Während "reaktive" Tiere sich daraufhin in die entgegengesetzte Ecke ihres Käfigs zurückzogen und dort inaktiv verharrten, vergruben "Proaktive" den Gegenstand unter dem Einstreu ihres Käfigs und setzten daraufhin ihre normale Aktivität fort; sie beseitigten also das Problem, während die "Reaktiven" diesem auswichen.

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