ANIMAL BEHAVIOUR, 2008, **76**, 1103–1105
doi:10.1016/j.anbehav.2008.08.008

IN FOCUS

Featured Articles in this Month's *Animal Behaviour*

Flying Over the Radar and Beyond Expectation

If there's one thing to be learned from the study of animal behaviour, it's that one should always expect the unexpected. No matter how carefully we build our models or how rigorously we design our experiments, we must always be prepared to change our views in light of the fact that animals can apparently achieve the impossible. The blue fin tuna, for example, can swim up to seven times faster than anatomical and physiological studies suggest is possible. Luckily, as the old joke goes, no one has told the tuna. By generating, and then exploiting, vortices in the water using their powerful tails, tuna can propel themselves much faster through the water and exceed their physiological limits. In this month's issue (pp. 1133–1138), Heiko Schmaljohann, Bruno Bruderer and Felix Liechti show that migrating songbirds are able to fly across the Sahara at temperatures that are much higher than expected, and which appear to exceed the birds' capacities to sustain continuous flight.

Songbirds crossing the Sahara desert are expected to fly at high altitudes in autumn to take advantage of cool and humid air. The disadvantage of this strategy is that they encounter head winds at high altitudes in autumn that impede flight and slow them down. Flying at low altitudes, however, where they would encounter beneficial tail winds, also exposes the birds to air that is hot and dry, resulting in heavy water loss. As most experiments have found that birds refrain from flying at all when temperatures climb above 25 °C, high-altitude flying has been assumed to be the norm. Schmaljohann and colleagues set out to test whether this was, in fact, the case by monitoring the flight of songbirds across the Sahara desert.

To obtain their measures, the researchers set up a radar site in Mauritania that could detect the birds as they flew overhead (Fig. 1). Moreover, they could identify birds as songbirds by their wing beat patterns. Birds passing over the site had already completed around 1500–1700 km of the 2000 km Sahara crossing. Contrary to prediction, these measures showed that songbirds chose to fly at altitudes that provided the best wind conditions, rather than those that minimized water loss. Over 60% of migration occurred at only 1000 m above ground level, where the temperature was around 30 °C. Schmaljohann and colleagues had calculated that the maximum possible overall water loss of a garden warbler, *Sylvia borin*, a typical trans-Sahara migrant, for the entire Sahara crossing would be in the order of 0.29 g/h, but found that songbirds passing over their study site must have lost something in the order of 0.62 g/h based on current knowledge of temperature-dependent water loss rates. With rates of water loss this high, birds should run out of water well before they have crossed the Sahara but, as these empirical data indicate, this isn't the case.

What, then, can explain these findings? Schmaljohann and colleagues have two suggestions: human error or bird adaptation. It is possible, for example, that putting birds in a wind tunnel or making free-flying birds carry equipment to measure physiological variables serves to increase the costs of flying, and hence leads to an overestimation of water loss. It's also possible that expired air may not be fully saturated with water, as most physiological models assume, so that rates of water loss may actually be lower than we have calculated. It is also the case that no experimental studies have actually been carried out above 25 °C. Any or all of these factors could explain why songbirds seem to achieve the impossible. If we can rule out experimental error, however, then the only alternative explanation is that songbirds must have some specific adaptations, much like the tuna's tail flicks, that allow them to sustain flight under hot conditions. It has been shown, for example, that

Figure 1. Heiko Schmaljohann using radar to track songbirds over the Sahara desert. Photo: Erich Bächler, Swiss Ornithological Institute.

0003–3472/08/$34.00/0

carrying large amounts of energy is less expensive for birds than previously thought, so perhaps birds also lose less water than expected. The birds may also possess some other physiological adaptations that only kick in at high temperatures and have therefore gone undetected so far. Either way, it is clear that these new data will have a profound influence on the development of future physiological models. They also emphasize the importance of studying animals in their natural environment, which allows us the possibility of detecting external, environmental factors that enable animals to augment and amplify their capacities in adaptive ways.

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Wary Elk Support the Risk Allocation Hypothesis

If you're edible, predation risk appears to be everywhere. Yet risk may vary both temporally and spatially. When predators are around, animals may allocate more time to antipredator vigilance. But how much? Animals may also avoid risky places to remain safe. But how does spatial variation in risk really affect behaviour? And, what happens when animals face both temporal and spatially variable risk? For instance, it is possible to be safer in cover only when predators are present and predators may not always be present.

Although antipredator behaviour has been studied for centuries, until recently, we had no quantitative theory to predict how both temporal and spatial variation in predation risk should influence antipredator behaviour. Around a decade ago, Steve Lima & Peter Bednekoff (1999) developed such a theory, which they called the 'risk allocation hypothesis'. This predicts that antipredator behaviour should be particularly sensitive to risk variation. For animals living in generally safe environments, a pulse of increased risk should lead to a larger antipredator response than for animals living in a risky area. This makes sense because animals in a safe area can expect a return to safe conditions quickly once the pulse of predation risk decreases, whereas animals living in a risky area should expect risk to persist beyond the current high pulse. In a safe world, selection would favour those who dropped everything during a rare period of risk. In a generally risky world, this luxury is not an option.

Until now this hypothesis has been tested only on animals in captivity. In this issue (pp. 1139–1146), Creel et al. provide a strong test of the risk allocation hypothesis under natural field conditions. They focused on elk, *Cervus elaphus*, living under risk of predation by wolves, *Canis lupus*, in what has become a remarkable natural laboratory of risk: the Greater Yellowstone Ecosystem.

Creel et al. studied elk that were either regularly exposed to wolves in the Northern Range, were intermittently exposed in the Gallatin Canyon, or were never exposed to wolves in the Elkhorn Mountains. As elk do not migrate between these patches during the course of a winter, Creel et al. could compare elk that lived under different background levels of predation risk. Additionally, while wolves might have been present in an area, the elk didn't necessarily encounter them on a daily basis. Over four winters, Creel et al. quantified both wolf activity and elk vigilance. They used a mix of radiotelemetry and reading signs (tracks, scats and fresh kills) to determine whether elk had experienced recent wolf exposure.

Creel et al. then explicitly evaluated alternative models to explain patterns of vigilance. Specifically, they compared the risk allocation hypothesis with a null model (vigilance should not be influenced by levels of risk), the risky times hypothesis (vigilance should be higher during pulses of risk), and the risky places hypothesis (vigilance should be higher in higher-risk areas than lower-risk areas). Their results provided strong support for the risk allocation hypothesis, some support for the risky times hypothesis, but no support for either the risky places hypothesis or the null model (Fig. 2).

In addition to providing some of the strongest support for the risk allocation hypothesis, there is an important ecological lesson to be learned from this study. Much research assumes that the ecological impact of predation can be assessed via knowledge of the number of times that prey encounter predators in a particular location. The current study, however, highlights the fact that, to understand both the spatial and temporal patterns of predation risk, we need to quantify the relative effect of behaviourally mediated risk. And, as Creel & Christianson (2008) point out elsewhere, responding to the risk of predation could lead to larger demographic effects than the

Figure 2. Elk, especially females, become more vigilant on days that wolves are locally present. Photo: John A. Winnie, Jr.

act of predation (specifically, the behavioural effects should be biggest when predators are rare enough to be largely avoidable).

Daniel T. Blumstein
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