

IN FOCUS

The physiology of predator stress in free-ranging prey



A 12-hours-old snowshoe hare born during the stress manipulation experiments. Photo by Jeffery R. Warner.

M.J. Sheriff, C.J. Krebs & R. Boonstra (2009) The sensitive hare: sublethal effects of predator stress on reproduction in snowshoe hares. *Journal of Animal Ecology*, **78**, 1249–1258.

Ecologists have only begun to understand the physiological mechanisms underlying individual- and population-level responses of prey- to predator-related stress. Sheriff, Krebs and Boonstra advance this field by providing evidence that predator-induced increases in glucocorticoid concentrations in wild female snowshoe hares (*Lepus americanus*) impact both litter size and offspring condition. They hypothesize that the glucocorticoid-mediated effects on reproduction provides an adaptive benefit: mothers ‘programming’ their offspring to be timid and risk-averse in high-risk environments should increase their survival probability. This research illuminates the connection between stress physiology and population-level changes and demonstrates the surprisingly far-reaching impact of predation risk.

Although a predator’s most obvious community impacts involve their consumption of prey, great progress has also been made in understanding the sublethal consequences of predation. Across a wide array of taxa, predation risk can induce changes in prey behavior and/or morphology that alter an organism’s activity and habitat use, foraging rate, growth, reproduction and other traits (reviewed in Preisser & Bolnick 2008). Although sometimes subtle on an individual level, these changes (‘nonconsumptive effects’) typically affect many more individuals than are directly consumed by predators (‘consumptive effects’). As a result, the population- and community-level consequences of nonconsumptive

effects can equal or exceed that of consumptive effects (Pangle, Peacor & Johannsson 2007; Creel & Christianson 2008; Schmitz 2008). Research in this area has proceeded along a variety of fronts and involved organisms ranging from *Daphnia* (Riessen 1999) to tadpoles (Fraker *et al.* 2009) to elk (Creel, Winnie & Christianson 2009). In particular, increased recognition of the large-scale importance of nonconsumptive effects has dovetailed with rapid progress in understanding the physiological mechanism(s) underlying an organism’s response to predation risk or other stressors. In vertebrates, this ‘stress response’ involves the activation of the hypothalamic–pituitary–adrenal axis and leads to increased glucocorticoid production. As glucocorticoid concentrations rise, organisms enter an ‘emergency state’ involving both

behavioral and physiological changes (Wingfield *et al.* 1998; Blas *et al.* 2007). These changes increase the organism's chance of survival but might involve a tradeoff between current reproduction and mortality risk (Wingfield & Sapolsky 2003). Interestingly, increased glucocorticoid concentrations may not always act as a causal mechanism: recent research into elk (*Cervus elaphus* L.) failed to detect a similar relationship between glucocorticoids and reduced reproduction (Creel *et al.* 2009). Although glucocorticoid-related changes in reproduction have been explored in a variety of laboratory experiments, Sheriff, Krebs & Boonstra (2009) take this work a step further by demonstrating that predator-related stress in free-ranging snowshoe hares (*Lepus americanus*) increases glucocorticoid concentrations and affects reproduction. Because snowshoe hares have been intensively studied as a model system for mammalian population cycles (Krebs *et al.* 2001a), their research thus provides evidence critical to linking individual-level physiology with community- and ecosystem-level processes (Boonstra *et al.* 1998; Krebs, Boutin & Boonstra 2001b).

Sheriff *et al.*'s findings emerge from two separate avenues, the first a large-scale monitoring survey and the second an experimental manipulation. Over a 3-year period starting at peak hare density and ending in the decline phase, they used a combination of live traps and track counts on two 36-ha grids to assess both predator (lynx and coyote) and hare densities in a boreal forest (for details of the system, see Krebs *et al.* 2001b). During the first and second snowshoe hare litters of each year, they also live-trapped 30 pregnant females and placed them in small individual outdoor pens (in order to protect the mothers from predators) within a large outdoor enclosure until they gave birth. In addition to recording the litter size and each leveret's condition, they also analysed maternal fecal samples taken 30 h following the birth for fecal cortisol metabolites, an indicator of maternal glucocorticoid concentrations. They found that metabolite concentrations decreased sharply between the first and second litters in each of the 3 years, and were inversely correlated with increases in both litter size and leveret condition. Predation risk decreased and food supply increased over this same period, suggesting that the waning of one or both of these potential stressors reduced metabolite concentrations and increased reproductive output. The second, experimental, part of their research involved capturing near-birth females, taking baseline measurements of the fecal cortisol metabolites, and then assigning them to large pens in the presence or absence of predator risk (a trained dog) until they gave birth. Litter size and leveret condition was then assessed, along with post-birth metabolite concentrations. Although litter size did not differ between the two groups, they found that stressed dams gave birth to lighter and smaller offspring and that maternal fecal cortisol metabolites were negatively correlated with offspring condition. In combination with the results from the large-scale survey, they conclude that predation risk (or another stressor) that increases glucocorticoid concentrations will reduce reproductive output.

In addition to making a solid case for the linkage between predator risk, increased glucocorticoid concentrations and reduced reproduction in free-ranging hares, Sheriff *et al.* evaluate several hypotheses for why such an apparently maladaptive stress response might occur. From a fitness perspective, trading off current reproduction for increased survival is adaptive only if organisms that do so are likely to survive to the next breeding period (Lima 1998). This is not the case for snowshoe hares, however; over 70% of each breeding population is yearlings, and females have only a 42% chance of surviving the period between their first and second litters (Sheriff *et al.* 2009). Hares that delay reproduction are thus unlikely to survive long enough to benefit fitness-wise from their choice. As a result, a tradeoff between reproduction and survival seems unlikely to explain the observed results. The short life and hard times of adult hares also argues against the recently suggested 'maternal matching' hypothesis (Love & Williams 2008). This hypothesis emerges from research in which stressed female European starlings raising glucocorticoid-injected eggs had both higher survival rates and fledged higher-quality (but fewer) offspring than did stressed mothers with control eggs. Although ingenious, this hypothesis' invocation of future reproductive events as a means of compensating for the stressed mother's reduced brood size makes it unlikely to occur in snowshoe hares.

Assuming that the observed hormonal changes are in fact adaptive, Sheriff *et al.* ultimately favor the 'maternal programming' hypothesis. This posits that mothers can increase the likelihood of their offspring responding appropriately to stressor(s) present in their natal environment. Leverets born to predator-stressed mothers would thus be more likely to exhibit anti-predator behavior and survive to adulthood. This explanation draws on several lines of evidence regarding the hypothalamic-pituitary-adrenal axis, including the fact that it can be permanently altered in the pre- and perinatal life stages (Meaney, Szyf & Seckl 2007), that glucocorticoid concentrations and stress responses are higher in the offspring of stressed mothers (Hayward & Wingfield 2004) and that its activation can increase fearfulness, vigilance, dispersal ability and, ultimately, survival (Meylan & Clobert 2005; Cabezas *et al.* 2007). Snowshoe hares do not shelter their young in burrows, and juvenile mortality rates are extremely high (O'Donoghue 1994); in such a situation, females that respond to stress by producing a smaller number of more fearful (and thus risk-averse) offspring might actually increase their fitness. This provides a plausible explanation for the paper's results, and an adaptive rationale for why maternal stress in snowshoe hares might yield fewer, smaller and more timid offspring.

The recent advances in snowshoe hare research highlight the fact that our understanding of the link between stress physiology and population-level processes is far more developed for vertebrates than for many other groups. At present, similar research on invertebrates has largely addressed the physiological underpinnings of growth-predation risk tradeoffs (Slos & Stoks 2008; Slos, Meester & Stoks 2009). While many invertebrates show a wide range of both

behavioral and physiological responses to predation risk (e.g. Beckerman, Wieski & Baird 2007), ecologists have just begun to explore the hormonal/chemical pathways that underlay morphological and life-history changes. Understanding the reproductive consequences of such changes is made even more challenging by the fact that many well-studied invertebrate taxa (e.g. insects such as damselflies, mayflies, butterflies and beetles) possess complex life cycles in which the immature stages are relatively sessile and occupy different habitats than do the wide-ranging adults. By laying out the protocols necessary to link individual- and population-level processes in a vertebrate system, Sheriff *et al.*'s paper should also spur ecologists to begin thinking about and testing similar hypotheses in non-vertebrate communities.

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