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Antipredator behavioural compensation of proactive personality trait in male Eurasian siskins

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Many animals show behavioural syndromes (i.e. suites of correlated behaviours across multiple situations). These behavioural correlations, however, imply limitations in the behavioural plasticity of individuals when facing the trade-off between predation risk and starvation risk. Some models suggest that proactive animals prioritize the reduction of starvation risk, while reactive animals do the opposite. Therefore, fast explorers that are also bold (i.e. proactive) are assumed to pay a predation cost associated with their behavioural trait. However, it has recently been suggested that proactive individuals may be able to compensate for their higher risk of predation by adopting some antipredator behaviours. In this study we tested these two alternative hypotheses with wild wintering Eurasian siskins, *Carduelis spinus*, foraging at artificial feeders. Male siskins have a melanin-based black bib that has been found to be correlated with exploratory behaviour, aggressiveness and dominance, and therefore is a signal of proactivity. We found that male siskins with large black bibs uttered more distress calls upon capture and displayed a vigilance strategy that improved predator detection. Moreover, this vigilance strategy did not reduce food intake rate. These results show that proactive individuals are not reckless, but instead compensate for their personality trait with stronger antipredator behaviours, and thus, do not necessarily have to pay a predation cost. Our results support the view of a positive relationship between eumelanism, proactive personality and the display of antipredator behaviours.

Recently, Sih, Bell, and Johnson (2004, p. 372) described a behavioural syndrome as 'a suite of correlated behaviors reflecting between individual consistency in behavior across multiple situations'. In accordance with this definition, some experimental studies and models have found a correlation between boldness and exploratory behaviour (Dammhahn & Almeling, 2012; van Oers, Drent, de Goede, & Van Noordwijk, 2004; Quinn & Cresswell, 2005; Wolf, van Doorn, Leimar, & Weissing, 2007) and a correlation between exploratory behaviour, aggressiveness and dominance (David, Auclair, & Cézilly, 2011; Mateos-González & Senar, 2012; Wolf et al., 2007). A behavioural syndrome, however, also limits the behavioural plasticity of animals confronting changing environmental conditions (Sih, Kats, & Maurer, 2003; Sih et al., 2004). Thus, a fast explorer that is also bold and aggressive (i.e. proactive; Sih et al., 2004) may suffer the consequences of its risk-taking behaviour in high predation risk situations (Jones & Godin, 2010; van Oers et al., 2004; Quinn & Cresswell, 2005).

Personality has a strong influence on the way animals face the trade-off between the risk of predation and starvation (e.g. Quinn, Cole, Bates, Payne, & Cresswell, 2011). It has been suggested that proactive animals prioritize the reduction of starvation risk, while reactive animals do the opposite (Biro & Stamps, 2008). Carter, Goldizen, and Tromp (2010) studying Namibian rock agamas, *Agama planiceps*, found empirical support for this hypothesis. Accordingly, in a recent review of the effect of life history strategy on fitness, bold individuals had higher productivity but with the handicap of a reduction in survival (Smith & Blumstein, 2007). In contrast, Jones and Godin (2010, p. 626) recently suggested that proactive individuals might have evolved antipredator behaviours to compensate for the higher risk of predation associated with their behavioural trait ('compensation hypothesis'). In line with this hypothesis, Godin and Dugatkin (1996) found that bold and conspicuous Trinidadian guppies, *Poecilia reticulata*, maintained greater escape distances from cichlid fish predators, while Carter, Marshall, Heinsohn, and Cowlishaw (2012) found no correlation between responses to a novel object and responses to a threat in wild chacma baboons, *Papio ursinus*. Couchoux and Cresswell (2012), studying redshanks, *Tringa totanus*, found no evidence of a behavioural syndrome related to risk management, and the only

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repeatable trait they found for this species was vigilance, which was adjusted in a flexible way to the riskiness of the situation. All these findings might explain the positive correlation between exploratory behaviour and survival (Smith & Blumstein, 2007) and the lack of a behavioural syndrome (Réale, Reader, Sol, McDougall, & Dingemanse, 2007, p. 305) reported for some species.

In line with the hypotheses formulated by Jones and Godin (2010), in the present study we tested whether proactive Eurasian siskins, *Carduelis spinus*, show a behavioural carryover leading to a reduction in antipredator behaviours (Sih et al., 2004) while keeping high food intake rates (Biro & Stamps, 2008; handicap hypothesis), or whether they evolved antipredator behaviours to compensate for the high risk of predation associated with their personality trait (compensation hypothesis). Siskins are socially foraging birds whose males have a melanin-based black bib that is a reliable signal of status, so that individuals with larger bibs are more dominant (Senar & Camerino, 1998; Senar, Camerino, Copete, & Metcalfe, 1993). The social system of this species is feudal, so that dominant individuals mainly fight each other and, therefore, are more aggressive than subordinates (Senar & Domènech, 2011). Moreover, male siskins with large black bibs are more exploratory (Mateos-González & Senar, 2012). Therefore, in this species we can classify males with large black bibs as having a proactive personality trait and males with small black bibs as having a reactive personality trait (Sih et al., 2004).

To test whether proactive or reactive siskins show more antipredator behaviours, we focused on vigilance behaviour, which significantly reduces the probability of capture (Lima & Dill, 1990), and on distress calls, which significantly increase the probability of escape from predators once captured (Conover, 1994; Laiolo, Tella, Carrete, Serrano, & López, 2004). We also examined reasons for departure from foraging and foraging bout lengths of the siskins. We observed a population of wintering siskins foraging at two feeders that differed in predation risk (high versus low). Short interscan durations are the best strategy to detect predators quickly, both in theoretical models (Hart & Lendrem, 1984) and in experimental studies (Whittingham, Butler, Quinn, & Cresswell, 2004). Moreover, siskins foraging in groups specifically reduce interscan durations with increasing predation risk (Pascual & Senar, 2013). According to the handicap hypothesis, large-bib siskins (proactive) should show (1) longer interscan durations, lower scan rates and/or lower percentages of time scanning, (2) fewer disturbance-related departures and (3) longer foraging bout lengths while feeding, especially at the high predation risk feeder, and (4) utter fewer distress calls once captured. In contrast, according to the compensation hypothesis, we would expect the opposite. In the present study we tested the above predictions and we also analysed food intake rates and aggression rates as well as the proportion of males of each bib size category on the two feeders as relevant variables to understand and interpret the results better.

METHODS

Model Species and Study Site

Wintering siskin populations are formed by resident and transient birds (Senar, Burton, & Metcalfe, 1992). Residents stay in the area for several weeks, whereas transients normally stay for a few hours or days. The usefulness of the black bib as a signal of status is especially relevant to transients, since residents have previous experience with one another and are dominant over transients (Senar, 2006). Therefore, in the present study we only selected transient birds (i.e. not colour ringed; see below) as focal individuals. The study was carried out in an area of orchards, small pine woods (*Pinus halepensis*) and gardens in the suburban area of Barcelona city (Catalonia, northeast Spain) from October 1996 to March 1997.

Bird Ringing and Videotaping

We captured siskins weekly from 19 October 1996 to 15 March 1997 (i.e. the wintering season) and marked them with numbered aluminium rings ($N = 584$). Birds that were recaptured repeatedly (i.e. stayed in the area as 'residents'; Senar et al., 1992) were also given unique colour ring combinations ($N = 104$), allowing long-distance identification. We placed two identical feeders (0.08 m wide, 1 m long) in the same area where a sparrowhawk, *Accipiter nisus*, routinely hunted (Pascual, Senar, & Domènech, 2014). One of the feeders was placed near protective cover (low predation risk feeder, LPF), and the other feeder was placed far from protective cover (high predation risk feeder, HPF). Mean ± SE group size was 9.10 ± 0.38 birds on the LPF and 7.87 ± 0.44 birds on the HPF (for more details, see Pascual & Senar, 2013). The feeders were filled with turnip, *Brassica rapa*, seeds, and birds foraging on them were simultaneously videotaped from a hide with two video cameras. We filmed only half the length of the feeders when videotaping, since they were too long to be recorded in the same image. Therefore, to prevent any biases and to increase the number of individuals recorded, we shifted the video camera every 2 min from one half of the feeder to the other half. In total, 27 flocks were recorded at feeders on 10 different days from 14 February to 11 March 1997, between 1000 and 1700 hours. The risk of predation at the area was real and high because we witnessed six attacks of a male sparrowhawk on birds foraging at the experimental feeders, and we found the remains of over 25 siskins caught by a predator in a pine wood within 20 m of the feeders (Pascual et al., 2014). The experimental design is validated elsewhere (Pascual & Senar, 2013), and we found that (1) 53% of the departures of focal siskins from the HPF were sudden departures of all or most of birds foraging at the feeder, usually after an alarm call, compared with 13% at the LPF, (2) 60% of the departures from the LPF were related to agonistic interactions, compared with 37% at the HPF, and (3) the proportion of time that siskins devoted to agonistic interactions was almost three-fold higher at the LPF than at the HPF. Therefore, we can confidently say that the perceived predation risk was much higher at the HPF than at the LPF and that aggression rates were much higher at the LPF than at the HPF. On the other hand, in the same study we found that siskins responded to an increase in predation risk by shortening interscan durations, whereas they responded to an increase in interference competition by lengthening scan durations.

Ethical Note

We captured siskins using Yunick platform traps, mist nets and clap nets. Yunick traps (Senar, 1988) consist of a platform feeder wrapped in wire mesh with a trap door on each side through which the birds gain access to the feeder. The trap doors are connected to a long rope, which, when pulled (from within a hide), causes the trap doors to fall down vertically and suddenly. Siskins captured in Yunick traps or clap nets were immediately removed and ringed, measured and released. Mist nets were visited every 0.5 h. The manipulation and ringing of siskins was carried out by expert bird ringers under the authorization of the Ornithological Catalan Institute. The capture of birds was carried out under the special authorization for scientific capture 206/97 from the Subdirecció General de Conservació de la Natura from the Departament d'Agricultura, Ramaderia i Pesca of the Generalitat de Catalunya.