



Stick or twist: roe deer adjust their flight behaviour to the perceived trade-off between risk and reward



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Because avoiding predation is crucial for fitness, foraging animals must trade acquisition of high-quality resources against risk avoidance when the best resources occur in locations with high predation risk. Although optimality models predict the distance at which an animal should initiate vigilance and flight, many studies have shown that animals generally flee soon after detecting an approaching threat, supporting the 'flush early and avoid the risk' (FEAR) hypothesis. Despite this, flight behaviour varies markedly depending on context, suggesting some behavioural plasticity in the response of prey to a given threat. We evaluated the degree of plasticity in the flight responses of roe deer, *Capreolus capreolus*, a highly flexible species which thrives in human-dominated landscapes. Based on individually identifiable animals and a standardized flight initiation protocol, we measured the distance at which a deer detected an approaching threat, and the distance at which it subsequently initiated flight. Our results provide strong support for the FEAR hypothesis, suggesting that alert and flight responses are strongly coupled in roe deer. However, the perceived level of both risk (in terms of landscape openness and proximity to human infrastructure) and reward (in terms of habitat quality) influenced the time it took for a deer to detect an approaching threat, and the subsequent time for which the threat was tolerated prior to flight. Overall, our findings indicate that although roe deer minimize monitoring costs when assessing risk by fleeing early, they also adjust their monitoring and flight responses to the local risk–resource trade-off.

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Optimal foraging theory states that foraging animals should strike a balance between maximization of energetic benefits and minimization of time spent to acquire a fixed amount of energy (MacArthur & Pianka, 1966; Pyke, Pulliam, & Charnov, 1977; Schoener, 1971), while simultaneously accounting for other constraints that potentially affect fitness. Prey species, such as ungulates, must trade acquisition of high-quality resources against predation or disturbance risk because the highest quality resources are often associated with high risk (Fraser & Huntingford, 1986; Sih, 1980). In a heterogeneous landscape of fear, prey are expected to minimize exposure to risk by adjusting their antipredator

behaviour to short-term changes in perceived predation risk (Laundré, Hernández, & Altendorf, 2001; Lima & Bednekoff, 1999; Lima & Dill, 1990). For example, vigilance is an antipredator tactic that allows individuals to exploit rich feeding patches, while concomitantly minimizing the probability of predation (Brown, 1999).

When encountering a predator, decisions made by prey are crucial for immediate individual fitness (Caro, 2005). For example, survival may be conditioned by the distance at which prey initiate flight from an approaching predator, i.e. the flight initiation distance (Fig. 1). Because human-induced stimuli are often analogous to predation risk for wildlife (Frid & Dill, 2002), measuring flight behaviour by experimentally approaching animals on foot offers a simple and reliable way to measure individual tolerance to perceived predation risk (Miller, Garner, & Mench, 2006; Tarlow & Blumstein, 2007). While flight behaviour has been shown to be a

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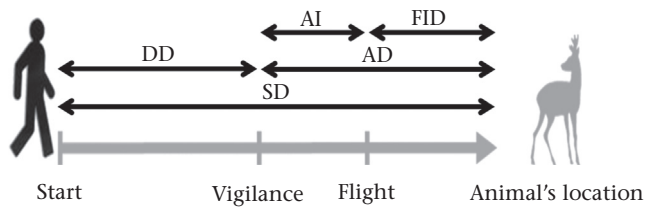


Figure 1. Schematic representation of a flight initiation distance approach depicting the distances measured as a function of the behavioural response of the focal animal: flight initiation distance (FID), assessment interval (AI), alert distance (AD), detection delay (DD) and starting distance (SD).

consistent and repeatable personality trait shaping how individuals distribute themselves in human-dominated landscapes (e.g. Carrete & Tella, 2010 on burrowing owls, *Athene cunicularia*), many studies on a variety of taxa have shown that animals can adjust their flight behaviour to the perceived level of predation risk (see review by Stankowich & Blumstein, 2005). For example, individuals may initiate flight earlier when approached in a faster and more direct manner (e.g. Cooper, 2009 on striped plateau lizards, *Sceloporus virgatus*; Stankowich & Coss, 2006 on Columbian black-tailed deer, *Odocoileus hemionus columbianus*) or when further from refuge habitat (e.g. Dill & Houtman, 1989 on grey squirrels, *Sciurus carolinensis*).

According to economic models of escape behaviour, flight initiation should occur when the costs of staying in terms of risk of death or injury equal the costs of fleeing in terms of loss of foraging opportunities (Cooper & Blumstein, 2014; Cooper & Frederick, 2007; Ydenberg & Dill, 1986). Both types of cost vary in space and time in response to factors that directly or indirectly affect the perceived level of predation risk, the prey's state and/or patch quality (Liley & Creel, 2008; Stankowich & Blumstein, 2005). Thus, a given threat may be perceived differently depending on environmental features (such as distance to refuge or landscape openness) and on characteristics of both prey (such as experience, age or reproductive status) and predator (such as the speed and directness of the approach). The observed flight response is thus shaped by how an individual perceives the risk of predation and how it trades foraging opportunities against risk avoidance. Blumstein (2003) and Stankowich and Coss (2006) refined this model to show, from both theoretical and empirical viewpoints, that animals assess costs and optimize their flight decision only when a predator is close enough to be detected and identified as a threat, but not close enough to provoke immediate flight.

The distances at which a predator starts its approach (starting distance) and when it is first detected (alert distance; see Fig. 1) are likely to be crucial in the flight decision of prey. In particular, flight behaviour depends strongly on the starting distance in many bird species (Blumstein, 2003). To explain why this might be so, Blumstein (2010) and then Cooper and Blumstein (2014) proposed the 'flush early and avoid the rush' (FEAR) hypothesis, which states that animals flee soon after they have detected a threat, to minimize the costs of monitoring an approaching predator in terms of lost foraging opportunities. According to this hypothesis, the distance at which a potential threat is detected (alert distance) and the distance at which that threat is no longer tolerated (flight distance) are strongly correlated because both monitoring costs and perceived risk increase as the assessment interval increases. The assessment interval describes the period following detection during which prey assess risk and decide when to flee depending on the cost–benefit balance of flight (see Fig. 1; Cooper & Blumstein, 2014; Fernández-Juricic, Jiménez, & Lucas, 2002; Stankowich & Coss, 2006). An individual's behavioural response to predation threat thus depends on the degree to which it tolerates a threat

once detected, but also on its ability to detect that threat in the first place. Probably because of the difficulty of reliably distinguishing vigilance in some species (Blumstein, 2010; Cooper, 2005), variation in detection delay and assessment interval have rarely been studied in the wild. However, the ability of prey to detect and monitor threats may have a marked impact on individual fitness because (1) detecting the predator too late may limit the anti-predator responses of prey and increase the risk of injury or death and (2) assessing the predator for an overly long time increases both the costs of lost foraging opportunities and predation risk, whereas fleeing immediately without assessing the risk can lead to an inappropriate antipredator response and energy loss (Cooper & Blumstein, 2014; Dugatkin, 1992; Quinn & Cresswell, 2005).

In this study, we investigated how variation in perceived risk and reward influence the detection, monitoring and flight behaviour of individually identifiable free-ranging roe deer, *Capreolus capreolus*, living in a heterogeneous human-dominated landscape where hunting is frequent. Assuming that prey should adjust their behaviour with respect to optimal escape theory, we investigated variation in the distance covered by an approaching observer prior to detection (denoted detection delay hereafter) and the subsequent distance covered before the focal individual fled (denoted assessment interval hereafter) in relation to both the quality of the habitat patch where the animal was foraging and the associated perceived predation risk. In terms of habitat quality, cultivated fields offer rich and concentrated food resources for roe deer. Hence, their exploitation should provide greater energetic rewards than natural meadows where preferred foods are less abundant and more dispersed (Hewison et al., 2009; Morellet et al., 2011). In terms of perceived risk, based on the available literature, we supposed that deer would perceive risk to be higher when foraging in more open landscapes, when far from woodland refuge habitat and when close to human infrastructure (e.g. see Benhaïem et al., 2008; Bonnot et al., 2013; Padié, Morellet, Hewison et al., 2015 for analyses on the same study site). Finally, although still a matter of debate (Stankowich & Blumstein, 2005; Stankowich, 2008), group size is generally expected to correlate negatively with risk perception in line with the many-eyes hypothesis (Lima, 1995; Pulliam, 1973) or because larger groups are more likely to contain at least one or more responsive individual(s) (Bonnot et al., 2015; Stankowich, 2008). We thus hypothesized that both the detection delay and the assessment interval should be shorter (1) in natural meadows, where perceived reward was assumed to be lower because of lower patch quality, than in crops, (2) in relatively open landscapes, far from woodland refuge and close to human infrastructure, when perceived risk was assumed to be higher, and (3) when group size was larger due to increased detection ability.

METHODS

Ethical Note

In our study site, roe deer have been caught during annual winter captures since 1996 in the context of a long-term ongoing project on roe deer ecology. During this study period (from 2010 to 2015), we captured and marked 237 roe deer (of which 16% were recaptured two to four times). Most caught animals were equipped with VHF or GPS collars ($N = 215$). All capture and marking procedures were done in accordance with French and European laws for animal welfare (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection). We used large-scale drives with 30–100 beaters and up to 4 km of long-nets. Roe deer were driven for a variable period lasting generally less than 10 min. Once a deer was

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