



Flight Initiation Distance and Starting Distance: Biological Effect or Mathematical Artefact?

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Abstract

In many studies, flight initiation distance (FID, the distance at which a prey starts to flee at the approach of a walker) is positively related to starting distance (SD, the distance at which the walker begins to approach) and alert distance (AD, the distance at which the focal individual becomes alert to the threat). In spite of the fundamental differences between SD, a covariate that may not have any biological effect, and AD, a measure related to the behaviour of the animal, it is common to use SD as a proxy for AD when AD is hard to measure (e.g. in species that do not exhibit distinguishable alert postures). However, the relationship between SD and AD or FID may not have any biological reasons, but may instead simply result from a mathematical artefact because of the constraints $SD \geq AD \geq FID$. Under such constraints, the homoscedasticity assumption is violated, and thus, the classical null hypothesis of linear regression (slope = 0) is invalid. In this study, we first show that using SD as a proxy for AD can strongly affect the results on FID. Using data from FID tests on alpine marmots (*Marmota marmota*), a linear mixed model with AD as a covariate, suggested that the interaction between previous activity and AD had an effect on FID, while this effect was not detected when SD replaced AD as the covariate in the analysis. We then propose that the actual statistical test of the relationship between SD, AD and FID should be based on a null hypothesis that incorporates the constraint $SD \geq AD \geq FID \geq 0$ and generate 95% CI of simulated slopes obtained from random values under this constraint. This null hypothesis can be rejected if the observed slope of the relationship between two of these variables is outside the 95% CI. We demonstrated that, for alpine marmots, the observed slope of the relationship between AD and SD was within the 95% CI of the simulated slopes. The absence of a statistically significant biological effect in the relationship between SD and AD raises important questions on the outcome of relationship between SD and FID. In Alpine marmot flight, decision should be studied separating the effect of SD on AD and the effect of AD on FID.

Introduction

Flight initiation distance (FID), the distance at which a prey starts to flee at the approach of a walker, is commonly used as a measure of the amount of risk perceived by an animal and has

been used to study the factors influencing the decision to flee (Ydenberg & Dill 1986; Blumstein 2003; reviewed by Stankowich & Blumstein 2005). To run a FID test, a person (referred to as the 'walker' hereafter) walks towards a focal animal under the assumption that the animal perceives the walker as

a threat similar to a real predator (Frid & Dill 2002). Cost-benefit models such as the economic model of flight (Ydenberg & Dill 1986) or the optimal FID model (Cooper & Frederick 2007, 2010) predict that FID will be optimized rather than maximized based on factors related to fitness tradeoffs of escaping or not. Compiling data on 68 species of birds, Blumstein (2003) found a strong positive relationship between FID and starting distance (SD), the distance at which the walker begins to approach. He suggested that this positive relationship was attributed to the fact that the cost of monitoring a predator increases with SD. Blumstein's model (2003) and the relationship between SD and FID have been taken into account in several recent FID studies (Blumstein et al. 2005; Geist et al. 2005; Cooper 2005; Stankowich & Coss 2006; Stankowich & Coss 2007; Cooper 2008; Cooper et al. 2009). SD is thus widely considered as an important parameter to include in FID analyses as it explains a large part of the variation in FID (Blumstein 2003). Escape theory assumes that prey decision to flee is based on predation risk assessment that is enhanced by monitoring the approaching predator (Ydenberg & Dill 1986; Cooper & Frederick 2007). Thus, if SD causes an increased cost of monitoring, prey must have detected the walker and consider the approaching human as a potential threat (awareness of the predation risk) when the approach begins. The flaw in this assumption is that it is almost impossible for the observer to measure when the walker was detected (Blumstein 2003; Fernandez-Juricic & Schroeder 2003). Moreover, some factors that may prevent detection such as animal posture (Krause & Godin 1996), orientation (Kaby & Lind 2003) and activity prior the start of the approach (Dukas & Kamil 2001) are not always considered in FID studies (e.g. Blumstein 2003; Blumstein et al. 2005; Cooper 2005; St.Clair et al. 2010). Thus, if detection is uncertain at the beginning of the approach (as in Blumstein 2003), the effect on FID of SD through an increased cost of monitoring is itself uncertain. Blumstein et al. (2005) and Boyer et al. (2006) propose instead to use alert distance (AD) as a measure of the detection delay. AD is the distance between the walker and the focal individual when the animal orients itself towards the walker and becomes noticeably alerted to the disturbance (Fernandez-Juricic & Schroeder 2003). A positive relationship between FID and AD has been found in several species (Cardenas et al. 2005; Gulbransen et al. 2006). Thus, previous studies (e.g. Fernandez-Juricic et al. 2005; Blackwell

et al. 2009) proposed to use AD rather than SD when AD is available, because: (1) only AD has a biological relevance related to the behaviour of the animal (Fernandez-Juricic & Schroeder 2003; Blackwell et al. 2009), and (2) SD should show a strong colinearity with AD (Fernandez-Juricic et al. 2005). However, in some species such as ambushers, no distinct alert posture can be observed by the experimenter, which prevents the measure of AD (Cooper 2005). In that case, it is appealing to use SD as a proxy for AD because these two measures are highly correlated even if authors recognized that SD is a covariate and not necessarily a biological effect (Stankowich & Coss 2006; Fernandez-Juricic et al. 2009). This practice is appropriate only under the assumption that controlling for SD instead of AD provides similar results. The test of this assumption is thus an important step in FID studies (Valcarcel & Fernandez-Juricic 2009).

Recently, Cooper (2008) and Blumstein (2010) pointed out that the relationship between SD and FID might be artifactual because spontaneous movements not motivated by escape can bias observation of flight under low predation risk and that the probability that an animal moves increases with SD and a longer duration of approach. They thus confirm that it is important to incorporate SD or AD in the study of FID to avoid this artefact. However, incorporating SD or AD in the study of FID can create another potential issue: the positive relationships between FID, AD, and SD can actually be caused by a simple mathematical artefact. By definition, FID is always smaller than AD when the animal responds to the approaching walker. In most studies (but see Stankowich & Coss 2006; Randler 2008), AD is smaller than SD (i.e. prey do not show alert behaviour prior approach starts) because walkers usually use precaution (slow and indirect approach) to avoid disturbing the animal before starting the test (Blumstein 2003; Blumstein et al. 2005; Fernandez-Juricic et al. 2005; Geist et al. 2005; Adam et al. 2006; Boyer et al. 2006; Eason et al. 2006; Gulbransen et al. 2006; Cooper et al. 2009). An animal that flees before the experiment starts can obviously not be included in an analysis on FID. The possible mathematical artefact is attributed to the relative distributions of SD, AD and FID. Even randomly chosen values of SD, AD and FID extracted from uniform distributions under the simple assumption that $SD \geq AD \geq FID$ (e.g. $SD \sim U(0,b)$; $AD \sim U(0,SD)$ and $FID \sim U(0,AD)$, where b is the largest possible value of SD) will almost always generate statistically significant positive relationships between the three variables (Fig. 1). This happens because, when

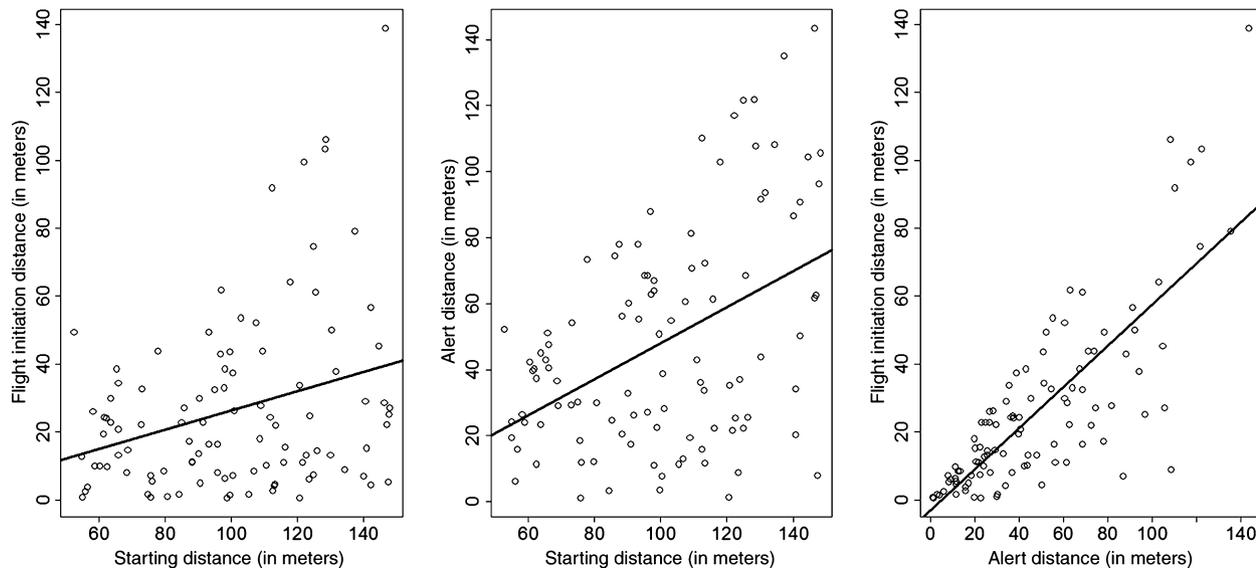


Fig. 1: Example of possible relationships between starting distance (SD), alert distance (AD) and flight initiation distance (FID) obtained from 102 simulated random values for each variable extracted from uniform distributions under the assumption that $SD \sim U(50,150)$; $AD \sim U(0,SD)$ and $FID \sim U(0,AD)$. The lowest and largest possible value of SD was arbitrary set to 50 and 150, respectively. We found positive and significant linear relationships between randomized SD, AD, and FID ($FID \sim SD$: $r^2 = 0.07$, $\beta = 0.24 \pm 0.09$, t -value = 2.69, $df = 100$, $p = 0.008$; $AD \sim SD$: $r^2 = 0.12$, $\beta = 0.40 \pm 0.11$, t -value = 3.72, $df = 100$, $p = 0.0003$; $FID \sim AD$: $r^2 = 0.52$, $\beta = 0.59 \pm 0.06$, t -value = 10.56, $df = 100$, $p < 0.0001$).

$SD \geq AD \geq FID$, the variables become heteroscedastic (i.e. increasing variances with larger values of the random variables) and thus the assumptions of linear regression are violated. Therefore, the positive relationship between SD, AD and FID may not have any biological relevance as the found relationships cannot be distinguished from those obtained from completely random numbers. To make sure that the relationships between SD, AD and FID are not a mathematical artefact caused by the constraint of size between the three distance parameters, we propose to test the positive relationships between SD, AD and FID under a null hypothesis that incorporates the constraint $SD \geq AD \geq FID \geq 0$.

In this study, we thus first test the assumption that SD is a good proxy for AD. Then, we propose to test whether the positive relationships between SD, AD and FID still hold after taking into account the spurious correlation because of the non-independence among those variables. Finally, we test the effect of biological factors (i.e. previous activity, distance to burrow and presence of conspecifics) on the slope of the relationships between SD, AD and FID. We exemplify its use by analysing data from FID tests on wild Alpine marmots (*Marmota marmota*). Finally, we recommend separating the effect of SD on AD, and the effect of AD on FID in studies on flight decision.

Methods

Study Area and Population

We carried out 102 FID tests on 37 individually marked Alpine marmots in the Orvielles study area, Gran Paradiso National Park, North-western Italian Alps (45°N7°E) during summer 2007 and summer 2008. We performed two to six tests per individual. Alpine marmots live in social groups formed by a dominant couple and their offspring up to 4 yr of age (Perrin et al. 1993). Members of a family group share and defend territories around their burrow systems (Perrin et al. 1993). The site, an alpine meadow located at 2165 m a.s.l., is frequently visited by tourists. According to the park regulation, visitors are restricted to using the trails in order to avoid disturbing the animals. Predators, including golden eagles (*Aquila chrysaetos*), red foxes (*Vulpes vulpes*) and wolves (*Canis lupus*), are present in the study area.

Field Methods

Individuals used for the study were captured and marked with coloured ear tags and fur bleaching to allow individual identification at a distance of up to 300 m. Each individual was marked with a unique

microchip transponder (Mod. Bayer Animal Coder) for long-term identification. Prior to a FID test, we identified an individual marmot with binoculars and a spotting-scope. An observer located at a distance of 100–300 m from the focal marmot measured SD as the distance between a walker and the marmot at the beginning of the test. We did not run the test if the marmot was alert before the walker started to walk (i. e. $AD > SD$) (following Blumstein 2003). We considered that a marmot was alert when it was standing on four legs, ready to run and with the head-up, so that it was possible to see the chest of the animal. SD was chosen to have a uniform distribution of distances ranging between 30 and 200 m. For short starting distances, the walker went closer to the focal marmot by approaching it very slowly, indirectly and avoiding facing it. The observer noted the location of the marmot prior to the test. After waiting a minimum of 60 s, the walker started walking at a constant speed (1.47 ± 0.37 m/s) in the direction of the focal individual. Constant speed of the predator is a common assumption in FID studies despite that the predators may use different strategies during approach. We used a chronometer to measure the time needed to walk the distance between SD and FID and estimated mean walking speed by dividing distance walked by time. While walking towards the marmot, the walker dropped a marker on the ground when the marmot first became alert and a second one when the marmot fled. Until the marmot did not disappear inside a burrow, the walker kept walking towards it. After the test, the observer measured SD, AD, and FID using the markers dropped by the walker. Measures were collected by the observer from a fixed observation point using the distance animal location method described in detail by Pasquaretta et al. (in press). A minimum period of 3 d elapsed between two tests on the same individual.

After the FID test, the observer noted the location of the burrow where the focal individual escaped. It was thus possible to measure the distance between the animal and its burrow before the walker started its approach. Bonenfant & Kramer (1994) observed that FID increased consistently with distance to the escape burrow.

Animals with at least one conspecific within 20 m were considered to be in the same group. The presence of a neighbour while foraging has been found to increase the chance to detect an approaching predator (Boland 2003; Randler 2008) and to increase dilution effects (Cresswell 1994; Quinn & Cresswell 2005).

We considered two categories of behaviour before the test: 'looking around' and 'foraging'. These two

behaviours are associated with different levels of risk (Blumstein 1998). A marmot that looked around usually laid flat on the ground with a 'head-up' posture. This behaviour is usually performed by individuals that are close to their burrow. Foraging marmots generally showed a 'head-down' posture with some rapid vigilance events (head-up). Compared with a foraging marmot, an individual looking around should detect a person faster, pay a low instantaneous cost of monitoring and reduce its risk of predation (Krause & Godin 1996). Alert behaviour during a FID test was distinguished from vigilance events because the marmot stood on its four legs, ready to run, head-up and it was possible to see the chest of the animal.

Statistical Analysis

First, we tested if the relationships between SD, AD and FID were best fitted by linear, logarithmic or quadratic functions as proposed in Stankowich & Coss (2006). A cubic function was tested for statistical significance if the quadratic relationship was preferred over the linear and the logarithmic function. A plateau or a drop in FID and AD is expected if, beyond a given distance, animals do not respond to an approaching threat, corresponding to the distance D_{\max} in Blumstein's model (Blumstein 2003). Individual marmots were tested repeatedly during the summers 2007–2010 (1–8 observations/individual). Individuals tested only once were not discarded from the sample because even if they generally reduce statistical power to detect variance among individuals (Martin et al. 2011), individual differences were not our point in this study. We ran linear mixed-effect models using FID as a dependent variable in linear, logarithmic or quadratic functions of the fixed effect SD. Individual identity was used as a random effect to account for repeated measures on each marmot. Our SD and AD values were all much higher than zero (min SD: 35 m; min AD: 13 m), and thus, we did not force the models to the origin as suggested in Cardenas et al. (2005). We selected the best fitted model by running a likelihood ratio test comparing linear models with logarithmic or quadratic models (Pinheiro & Bates 2000). If the p-value obtained was less than 0.05, we kept the model with the lower log-likelihood value. We repeated this methodology to test for the relationship between FID and AD, and AD and SD.

We tested the assumption that SD is a good proxy for AD by running two models, one that used SD and the other one AD as covariates for FID. SD can be considered as a good proxy for AD when the two models provide similar results. Otherwise, AD cannot be

replaced by SD without caution. We tested the effects on FID of AD and three commonly used variables in FID studies: activity prior to the walker approach (foraging or looking around), the distance to the closest burrow and the presence of conspecifics within a distance of 20 m from the tested animal. The interactions between AD and the other independent variables were used in the model. Mixed models were implemented in the statistical environment R (R Development Core Team 2011) using the lmer function of the lme4 package (Bates & Maechler 2010), and the function (mcmcsm) that generates a sample from the posterior distribution of the fixed effects parameters using a Markov Chain Monte Carlo approach. We thus checked that the 95% highest posterior density (HPD) intervals associated with each coefficient did not include zero. We then ran exactly the same model using SD as a proxy for AD.

Heteroscedasticity was observed in the regression between FID and both SD and AD. In other words, the variance in distances between start/alert and flight increased with larger values of SD or AD. In such case, heteroscedasticity limits the possibility to observe significant effects on FID (i.e. activity, distance to burrow, presence of conspecifics). This result is consistent with Blumstein's model (2003). The presence of heteroscedasticity in our models may be of biological interest (Cleasby & Nakagawa 2011). In some FID studies, heteroscedasticity is kept in analysis (Cooper 2005; Fig. 1; Cooper 2008; Fig. 1).

Testing Statistical Significance of the Slope in Relationships Between SD, AD and FID

To test whether the strong positive relationships between SD, AD, and FID are simply caused by a mathematical artefact or reflect some biological phenomena, we propose to compare the observed slope of the relationship between two of these variables with slopes obtained from simulated random variables (FID_s and AD_s) sampled from a uniform distribution. For the three possible relationships between SD, AD, and FID ($FID_s \sim SD$; $FID_s \sim AD$; $AD_s \sim SD$), we generated 1000 estimates of the slope using simulated random uniform distributions of AD_s and FID_s (the dependent variables in the mixed-model analyses). We kept the same sample size in each simulations ($n = 102$) than in the observed database. Each individual was attributed simulated AD_s and FID_s values, based on observed values of SD and AD, respectively. We constrained the simulated AD_s and FID_s data so that $SD \geq AD_s \geq 0$ and $AD \geq FID_s \geq 0$. For each relationship between two variables, we estimated the

95% confidence interval from the Monte Carlo simulation estimates and tested if the observed slope of the regression was included within the 95% CIs. An observed slope included in the 95% CI indicates that the positive relationship between the two distances is not distinguishable from the relationship, which would be obtained from completely random uniformly distributed data. In this situation, it is thus not possible to infer any biological effect on the relationship between the two variables (Mooney 1997; Rubinstein 2009; Tuffin 2010). In contrast, a slope value outside the 95% CI indicates a possible biological interpretation of the positive relationship between the two distances. We then ran a series of linear models that included one biological factor at a time (i.e. previous activity, distance to burrow or presence of conspecifics) and compared the observed slope for each treatment with a random slope under the constraint $SD \geq AD \geq FID \geq 0$.

This method can be extended to situations where individuals have been observed several times. In this case, because of repeated observations on some individuals, we can use linear mixed models to obtain the observed and simulated values of slopes between two variables, using individual as grouping factor. The R code used for this analysis is provided in the Appendix S1.

Results

Relationships Between FID, AD, and SD

Relationships between FID and both SD and AD were best fitted by a linear function ($FID \sim SD$: $\beta = 0.57 \pm 0.06$, t -value = 9.02; $FID \sim AD$: $\beta = 0.87 \pm 0.04$, t -value = 23.37). The linear and the logarithmic models did not differ significantly (likelihood ratio test; FID vs. SD: $\logLik_{\text{linear}} = -473.16$; $\logLik_{\text{log}} = -474.44$; $\chi^2 = 0.00$; p-value = 1; FID vs. AD: $\logLik_{\text{linear}} = -408.33$; $\logLik_{\text{log}} = -435.78$; $\chi^2 = 0.00$; p-value = 1). A logarithmic function model ($AD \sim \log(SD)$: $\beta = 64.31 \pm 6.88$, t -value = 9.36) was most appropriate for the relationship between AD and SD ($\logLik_{\text{linear}} = -477.72$; $\logLik_{\text{log}} = -476.81$; $\chi^2 = 1.83$; p-value < 0.0001; $\logLik_{\text{quadratic}} = -415.71$, $\chi^2 = 0.92$; p-value = 0.34). We did not fit the quadratic model when the relationship was best fitted by the linear function.

Linear Mixed Models

The linear mixed model using AD as a covariate suggested that an interaction between previous activity

and AD had an effect on FID, but, this effect was not detected when SD replaced AD as the covariate in the analysis (Table 1). Thus, using SD as a surrogate for AD would have prevented us from noticing that, for a given AD, FID was greater when animals were foraging at the start of the test than when they were looking around. Moreover, when SD was introduced in the model instead of AD, we found a positive effect of the distance to burrow and the interaction between distance to burrow and SD on FID (Table 1). The effect of the presence of conspecifics was not significant in any model.

Testing Statistical Significance of the Slope in Relationships Between SD, AD and FID

Both observed relationships between SD, AD and FID (FID ~ SD: $\beta = 0.57$; FID ~ AD: $\beta = 0.87$), and our random simulations produced positive and significant relationships (FID_s ~ SD: 95% CI = 0.18–0.42; AD_s ~ log(SD): 95% CI = 35.05–67.47; FID_s ~ AD: 95% CI = 0.32–0.67) (Table 2; Fig. 2). The observed slope of the relationship between AD and SD (AD ~ log(SD): $\beta = 64.31$) was within the 95% CI of the simulated slopes (Table 2). The observed slopes between SD and FID and between AD and FID were outside the 95% CI of the simulated slopes (Table 2).

The constraint that SD \geq FIDs generated a 95% CI ranging between 0.18 and 0.42. The observed slope of

Table 1: Effects of AD and SD, other variables and interactions on FID in alpine marmots. In parentheses, the variable of reference in the coefficient of regression for categorical effects. 95% highest posterior density (HPD) is the 95% highest posterior density intervals for the coefficients. Variables with statistically significant effects (zero is not included in the interval) are identified by two asterisks (**)

Models and variables	Estimates	95% HPD
FID ~ AD + variables + interactions		
AD**	0.96	[0.84; 1.08]
Activity (looking around)	5.5	[−7.07; 21.90]
Distance to burrow	0.22	[−0.05; 0.53]
Group (presence of conspecific)	−1.24	[−14.51; 10.41]
AD:Activity (looking around)**	−0.23	[−0.39; −0.07]
AD:Distance to burrow	−0.003	[−0.006; 0.0007]
AD:Group (presence)	0.03	[−0.09; 0.16]
FID ~ SD + variables + interactions		
SD**	0.82	[0.62; 1.05]
Activity (looking around)	10.99	[−16.72; 58.57]
Distance to burrow**	0.84	[0.16; 1.48]
Group (presence of conspecific)	7.71	[−22.17; 37.95]
SD:Activity (looking around)	−0.21	[−0.57; 0.05]
SD:Distance to burrow**	−0.009	[−0.01; −0.002]
SD:Group (presence)	−0.03	[−0.20; 0.28]

Table 2: Observed slopes of the relationships between FID, SD and AD in Alpine marmots, and 95% CI for the slopes obtained from simulated random data. An observed slope outside of the 95% CI indicates that the observed relationship is not only explained by a mathematical artefact between the variable caused by the constraint on their respective distributions

Relationship	Observed slope	95% CI from simulated random data ^a	Observed slope outside the 95% CI of random slopes
FID ~ SD	0.57	0.18–0.42	>
AD ~ log(SD)	64.31	35.05–67.47	No
FID ~ AD	0.87	0.32–0.67	>

^a95% CI was obtained from 1000 estimates of the slope of the relationship between SD, AD and FID, using simulated random uniform distribution of the dependent variables, AD_s and FID_s. The simulated AD_s and FID_s was constrained so that SD \geq AD_s \geq 0 m and AD \geq FID_s \geq 0 m (see Method for more details).

the relationship between SD and FID was inside the 95% CI when the animals were looking around (FID_{looking around} ~ SD_{looking around}: $\beta = 0.39$) (Fig. 3). The slope was outside 95% CI when the animals were foraging (FID_{foraging} ~ SD_{foraging}: $\beta = 0.60$), when distance to burrow was controlled for (FID_{burrow} ~ SD_{burrow}: $\beta = 0.57$), and when the animal was either alone (FID_{alone} ~ SD_{alone}: $\beta = 0.54$) or in presence of a conspecific (FID_{group} ~ SD_{group}: $\beta = 0.61$).

The constraint SD \geq AD generated a 95% CI ranging between 35.05 and 67.47. The observed slope between SD and AD was slightly inside the 95% CI when animals were foraging (AD_{foraging} ~ log(SD)_{foraging}: $\beta = 67.4$), but could not be considered as different from a random slope when animals were looking around (AD_{looking around} ~ log(SD)_{looking around}: $\beta = 49.8$), when distance to burrow was controlled for (AD_{burrow} ~ log(SD)_{burrow}: $\beta = 64.5$), and when the animal was either alone (AD_{alone} ~ log(SD)_{alone}: $\beta = 63.5$) or in presence of conspecifics (AD_{group} ~ log(SD)_{group}: $\beta = 63.2$) (Fig. 4).

The constraint AD \geq FIDs generated a 95% CI ranging between 0.32 and 0.67. The observed slopes of the relationship between AD and FID were all outside the 95% CI (FID_{looking around} ~ AD_{looking around}: $\beta = 0.69$; FID_{foraging} ~ SD_{foraging}: $\beta = 0.91$; FID_{burrow} ~ AD_{burrow}: $\beta = 0.87$; FID_{alone} ~ AD_{alone}: $\beta = 0.85$; FID_{group} ~ AD_{group}: $\beta = 0.89$) (Fig. 5).

Discussion

FID increased linearly in the same way with AD and SD. However, on the one hand, including AD in the model allowed us to detect the effect of initial activity on FID, and on the other hand, using SD allowed us

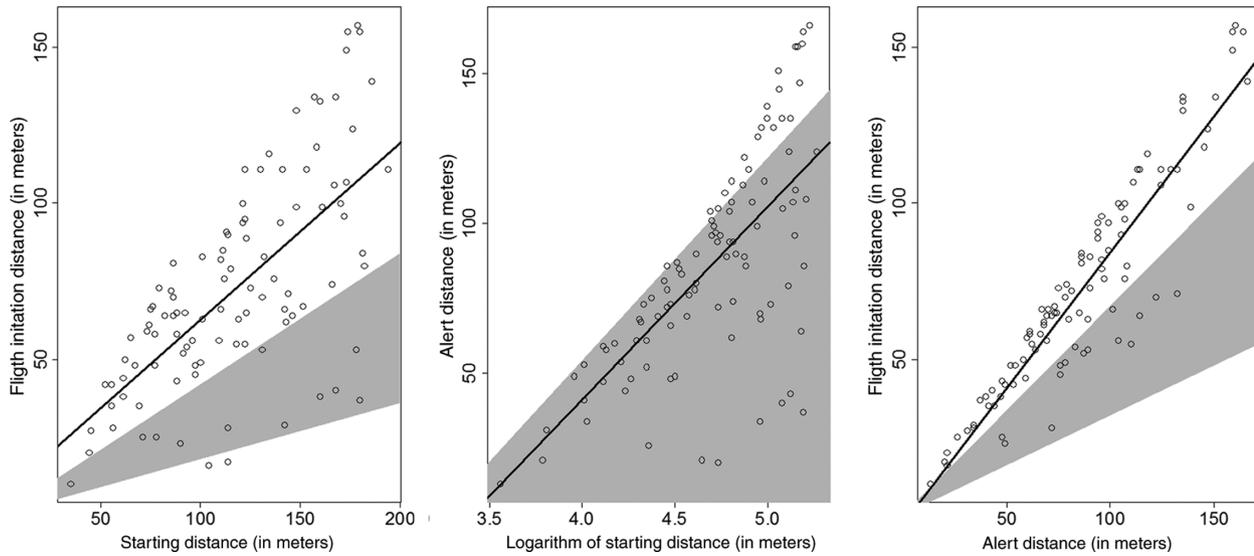


Fig. 2: The relationship between starting distance (SD), alert distance (AD) and flight initiation distance (FID) in Alpine marmots in Orvielles, Gran Paradiso National Park, Italy. The shaded zone represent the 95% confidence interval from the Monte Carlo simulation estimates. A slope value outside the 95% CI indicates a possible biological interpretation of the positive relationship between the two distances.

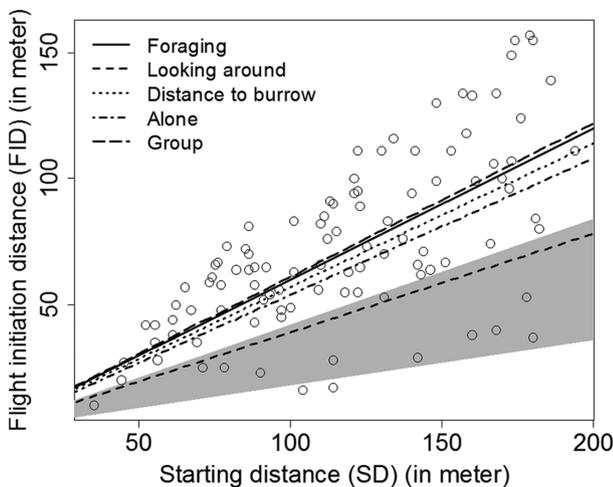


Fig. 3: The relationship between starting distance (SD) and flight Initiation distance (FID) for each treatment (i.e. previous activity, distance to burrow, presence of conspecifics) in Alpine marmots in Orvielles, Gran Paradiso National Park, Italy. The shaded zone represent the 95% confidence interval from the Monte Carlo simulation estimates. A slope value outside the 95% CI indicates a possible biological interpretation of the positive relationship between the two distances.

to detect an effect of the distance to burrow on FID. In the AD model, we found that, for a given AD, FID was shorter when the marmot was looking around than when it was foraging. In contrast, in the SD model both distance to burrow and its interaction with SD had a significant effect on FID. In general, studies on FID use SD when AD is not observable (e.g. Cooper

2005, 2006, 2008; Fernandez-Juricic et al. 2009). This decision is based on the assumption that SD can be used as a proxy for AD because SD and AD are usually strongly correlated. In our study, SD did not appear to be an adequate proxy for AD, confirming criticisms on SD made by previous studies (Fernandez-Juricic et al. 2005; Blackwell et al. 2009; Valcarcel & Fernandez-Juricic 2009). Our example on Alpine marmots also showed that the mathematical artefact alone can explain the positive relationship between SD and AD. In contrast, it is possible that some biological factors in addition to the mathematical artefact played also a role in the positive relationship between FID and both SD and AD. As any other statistical methods, it is highly probable that the chance of type II error depends on sample size.

Biological factors (i.e. activity of the animal prior to the test) had an effect on the slope of the relationships between SD, AD and FID. In Alpine marmot, the slope of the relationship between SD and FID and between SD and AD were not statistically significant when animals were looking around, but were outside the 95% CI when animals were foraging. An observed slope outside the 95% CI indicates that the relationship between SD and AD, or FID cannot be explained by the constraint of size between the three distances parameters and may thus indeed be related to biological factors. In this case, the positive relationship between SD and FID may be caused by the increasing cost of monitoring a predator with SD (Blumstein 2003) or by an increased probability of spontaneous

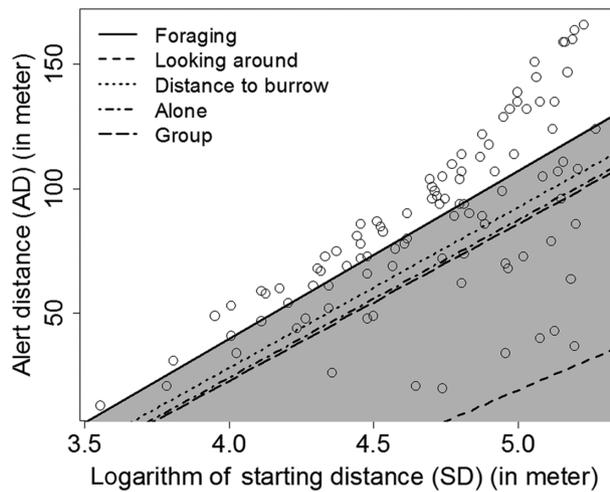


Fig. 4: The relationship between logarithmic of starting distance (SD) and alert distance (AD) for each treatment (i.e. previous activity, distance to burrow, presence of conspecifics) in Alpine marmots in Orvilles, Gran Paradiso National Park, Italy. The shaded zone represent the 95% confidence interval from the Monte Carlo simulation estimates. A slope value outside the 95% CI indicates a possible biological interpretation of the positive relationship between the two distances.

movements with a duration of approach (i.e. duration of the approach increases with SD) (Cooper 2008; Blumstein 2010). The influence of activity on the slope of the relationships could be caused by the effects of activity on the cost of monitoring or a loss of opportunities.

The cost of monitoring is affected by the frequency with which the animal switches from foraging (or other activities) to vigilance, or by the loss of opportunities when limited cognitive attention is directed towards the walker instead of a prey (e.g. an ambusher monitoring the approach of a walker can miss opportunities to catch a prey). Once the walker is detected, the cost of monitoring increases with time and attention devoted to monitoring and reaches a maximum when the animal quits its previous activity to adopt alert posture (to enhance monitoring and get ready to flee) (Fig. 6). At AD, the cost of monitoring is at its maximum regardless the distance separating the walker and the prey. Our results indicate that the cost of monitoring differs between activities. The head-down posture of a foraging Alpine marmot prevents monitoring and foraging simultaneously. Thus, the cost of monitoring increases quickly once a foraging animal detects the approaching walker. However, an animal that is looking around pays negligible costs associated with monitoring the approaching walker. The detection of the presence of the walker may not be enough to cause a change in prey vigilance behav-

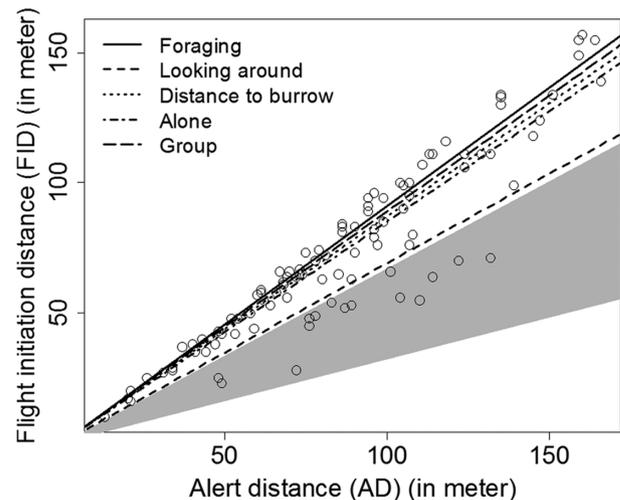


Fig. 5: The relationship between logarithmic of alert distance (AD) and flight initiation distance (FID) for each treatment (i.e. previous activity, distance to burrow, presence of conspecifics) in Alpine marmots in Orvilles, Gran Paradiso National Park, Italy. The shaded zone represent the 95% confidence interval from the Monte Carlo simulation estimates. A slope value outside the 95% CI indicates a possible biological interpretation of the positive relationship between the two distances.

our. Stankowich & Coss (2006) proposed that animals may detect a predator but they do not consider it as a threat beyond a zone of awareness. They suggested that the zone of awareness can differ based on possible different evaluation of risk by the prey. A prey increases its awareness of the walker if the behaviour of the latter increases the likelihood for the prey to be attacked (Cooper et al. 2003; Stankowich & Coss 2006). Cooper et al. (2009) showed that the level of risk (represented by the difference in approach speed) may influence the relationship between SD and FID. In both approaches (slow and fast), the walker had equal chances to be detected, but a fast and direct approach is a non-ambiguous signal of an attacking predator, which may not be the case for a slow approaching walker. Thus, detection and monitoring of the approaching walker is possible before the animal exhibits alert posture, but the cost of monitoring depends on biological factors (e.g. activity, walker behaviour).

Some biological factors may affect the relationship between SD and FID, but only because of the strong effect of AD on FID and the strong correlation between AD and SD. The distance walked by the walker from SD to FID includes both the distance walked from SD to AD and the distance walked from AD to FID (i.e. $(SD - FID) = (SD - AD) + (AD - FID)$). Thus, the positive relationship between SD and FID is the addition of both effect of SD on AD and

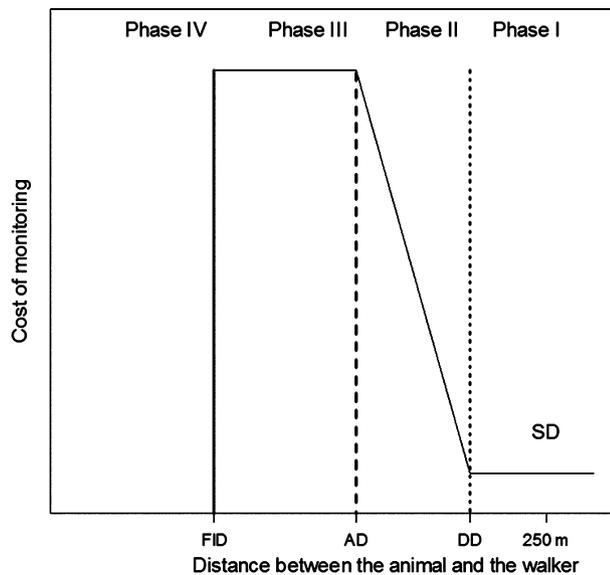


Fig. 6: Schematic representation of timeline of prey vigilance and escape behaviour during a predator-prey encounter. The whole approach is decomposed into four successive phases (i.e. I to IV) separated by three threshold events. The first threshold corresponds to the detection of the predator by the prey (DD; dotted-line). As the prey does not signal that it has detected the presence of the predator, observer could be unable to determine that threshold event (e.g. Blumstein 2003). For the second, the prey shows an alert behaviour (AD, dashed line). In the third, the prey decides to flee (i.e. flight initiation or FID, full line). In phase I, the prey resumes beneficial activity (e.g. foraging, mating) interrupted by bouts of vigilance, but these bouts of vigilance are not related to the approach by the predator because it has not been detected yet. Once it has detected the predator (phase II following DD), the prey increases its time spent vigilant. The increase in the time devoted to vigilance increases the cost of monitoring (or lost of opportunity). In phase III, the cost of monitoring reaches a maximum as the animal switches from beneficial activity to continuous monitoring of approaching walker. The continuous monitoring enhances risk assessment, which leads to an optimal escape decision. In phase IV, the prey flee from the predator, escaping to a safe area or a refuge. The relative importance of the different phases depends greatly on several factors such as the starting distance, the activity of the prey and the prey ability to detect the approach by the predator (i.e. body orientation and posture, prey visual acuity and habitat characteristics).

effect of AD on FID. The absence of a biological effect in the relationship between SD and AD raises some doubts about the outcome of relationship between SD and FID. Relationships between FID and SD could be influenced by factors such as vigilance bouts that may not be involved in the optimization of FID, but could affect it through their effects on the ability to detect the predator and therefore on AD (Fernandez-Juricic & Schroeder 2003). Distance to the refuge can increase vigilance (Unck et al. 2009). In Alpine marmots, distance to the burrow affected the relationship between SD and FID, but not between AD and FID.

This result suggests that the effect of distance to burrow could only have an effect on AD through an effect on the vigilance behaviour and, thus, the abilities to detect the walker. Moreover, non-escape (spontaneous) movements (Cooper 2008) are likely to increase with SD in the zone between SD and AD because the prey may not have detected the approaching walker.

A given factor can have antagonistic effects on AD and FID, and therefore by not considering AD in a FID study one can miss important parameters affecting anti-predatory behaviour. For example, an animal in a larger group can detect a predator earlier (Boland 2003) and then increase both AD and consequently FID (Randler 2008). On the other hand, being in a larger group increases the risk dilution effects (Cresswell 1994; Quinn & Cresswell 2005). As a result of dilution effects, an animal alerted by the approach of a predator should delay its escape (i.e. decreases its FID). Fernandez-Juricic et al. (2002) observed that the difference between alert and flight distances (AD – FID) increased with group size in four birds species: house sparrows (*Passer domesticus*), magpies (*Pica pica*), black-birds (*Turdus merula*) and wood pigeon (*Columba palumbus*). This could be explained by the dilution of risk predation in larger groups. Stankowich (2008) reported extremely high heterogeneity in the effect of groups size on flight decisions in ungulates. This could be the results of the antagonist's effects of groups size on AD and FID. However, in Alpine marmots, the presence of conspecifics had no effect either on AD or on FID.

The linear shape of the relationship between FID and SD (or AD) suggested that the current dataset and simulation appears to test values within a zone of trade-offs where cost of remaining and cost of flight influence decision to flee (referred as Zone II in Blumstein 2003). This shape depends upon the range of SD and AD tested and could be different if very large SD was used (Stankowich & Coss 2006). Thus, conclusions may have been different in such a case. However, testing costs and benefits of escape beyond D_{max} , a threshold distance beyond which prey never move away from an approaching predator (in zone III), may be biased if prey is not able to detect walker or does not assess predation risk at such long distance (Blumstein 2003). Thus, the use of SD in the appropriate range (zone II) is required to test optimization of flight behaviour adequately.

Our results point out a possible spurious interpretation of the relationship between FID, SD and AD. We thus suggest separating the effect of SD on AD and the effect of AD on FID. Using a Monte-Carlo approach is

only the first – although essential – step of a FID study, and researchers may make sure that their data set does not reduce the chance of detecting some important biological effects hidden behind their mathematical association. Simulations will be needed to investigate how the approach could be generalized to a wide range of scenarios and systems. The model proposed in Blumstein (2003) should be applied using the relationship between AD and FID because the assumption that SD generates a cost of monitoring is uncertain. However, the animal may adopt an alert posture prior to the start of the approach; or AD may be impossible to measure (some animal species never exhibit obvious alert postures) making it impossible to follow our recommendation. In some cases, AD may be considered equal to SD when the animal is already alert prior to the start of the approach (Stankowich & Coss 2006; Randler 2008). In such cases, SD may be used as a surrogate measure of AD because the animal exhibits an obvious detection of the walker and awareness of threat that cause a continuous monitoring of the approaching walker. Thus, similarly to AD, SD causes a cost associated with the switch from a fitness enhancement activity (e.g. foraging) to continuous monitoring. On the other hand, the absence of an alert posture does not mean that the animal can both forage and assess risks simultaneously. Dukas & Kamil (2000) observed that blue jays (*Cyanocitta cristata*) reduced peripheral target detection when engaged in a difficult central task (i.e. foraging). This is in conflict with Cooper's (2005) hypothesis that monitoring costs are absent in ambushers. In conclusion, when the aim of FID studies is to establish setback distance in wildlife conservation, and AD cannot be measured, we strongly recommended standardizing SD experimentally (e.g. using the same SD in all tests) to avoid any treatment effect and to control for factors involved in walker detection (i.e. scanning bouts, animal orientation, landscape) and awareness (i.e. approach speed, Cooper et al. 2003; Stankowich & Coss 2006; Cooper et al. 2009; directness of approach, Cooper et al. 2003; Stankowich & Coss 2006, quick movements, Cooper 1997, 1998; walker's body orientation; Cooper 1997, 1998; Blumstein 2003).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Monte Carlo simulations R code to correct for the potential mathematical artefact on the relationship between FID and both AD, and SD

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