

Project Proposal

The effect of predation risk on personality-dependent movement

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1 Introduction

It is commonly observed that individual animals often differ in their behaviour, leading to the idea that otherwise homogeneous groups might harbour significantly more diversity than previously thought. When animals show consistency in behaviour across contexts or over time (Sih et al. 2004a; Sih et al. 2004b), this may be classified as a personality, and can have important implications above the individual level (Sih and Bell 2008; Sih et al. 2012). A logical consequence of personality is finite behavioural plasticity, and hence non-optimality in some contexts (Wolf and Weissing 2010; Wolf and McNamara 2012).

To complicate matters further, individual consistency along behavioural axes such as exploration and boldness is often correlated to form a syndrome, and the relationship between the axes can be difficult to elucidate (Réale et al. 2007; Carter et al. 2013). This is especially true when animals are tracked in their natural environment where behaviour can only be remotely observed (Cooke et al. 2004; Kays et al. 2015) as the result of natural experiments, and not in response to controlled stimuli (Leclerc et al. 2016). Landscape-scale perturbation to test the existence, strength, and ecological effects of behavioural consistency is usually difficult to achieve in such systems.

Predation risk is somewhat of an outlier in landscape-level effects on behaviour, since a landscape of fear [of predators] (Laundré et al. 2001) is relatively easily established. Consequently, anti-predator responses are well known (Lima and Dill 1990), including spatio-temporal avoidance at landscape scales (e.g. Lank et al. 2003; Ydenberg et al. 2004). Optimality in avoidance at small spatio-temporal scales often takes the form reported by Kohl et al. 2018: prey eschew areas heavily used by predators at times of day when predators are most active, yet have no qualms about the same areas when predators are largely inactive. However, the binding of behavioural traits into a syndrome could result in non-optimal risk avoidance behaviour. For example, if exploration and risk avoidance were to be correlated to form a "bold" type, such individuals might use more of their landscape, and also have lower revisit intervals to the site of a predator attack. Individuals' internal state might be a confounding factor in teasing apart the correlation of exploration and risk-taking, in that individuals might accept the probability of predation over the certainty of starvation. Controlling for individual state would require knowledge of the resources consumed and thus information on intake.

Here, we propose a project suitable for a master's student with an interest in animal movement and strong data handling skills in R or another statistical language. The project takes advantage of a number of independ-

29 ently developed capabilities that can help investigate the effect of predation on landscape scale movement in
30 a population of individuals known to show consistent individual differences in exploratory behaviour.

31 First, the Bijleveld lab at the Department of Coastal Systems at NIOZ has a thorough understanding of
32 and unprecedented access to a large migratory population of shorebirds off the Dutch Wadden Sea island
33 of Griend. Specifically, around 150 red knots (*Calidris cantus*) are regularly caught each summer, marked
34 with coloured leg-rings, and a subset are fitted with ATLAS Time of Arrival tags (*unpublished data, Allert
35 Bijleveld*). These tags allow 0.25 – 1.00 Hz tracking in a 100 km² area around Griend for approximately
36 2 – 3 months after deployment (MacCurdy et al. 2015; Oudman et al. 2018). Further, the NIOZ Synoptic
37 Intertidal Benthic Survey samples the macrozoobenthic prey of red knots at a resolution of 250 m, which is
38 then transformed into a 10 m resolution landscape of predicted intake rates (Bijleveld et al. 2015; Bijleveld
39 et al. 2012; Oudman et al. 2018; Bijleveld et al. 2016). SIBES samples are taken in early and late summer
40 (July and October), when red knot densities are very different, which allows for a comparison of pre- and
41 post-occupation intake rates (see Bijleveld et al. 2015).

42 Second, the Hemelrijk lab at GELIFES-RUG has the technical skill to manipulate predation risk for large
43 flocks of birds, using a fixed-wing drone resembling a globally distributed raptor, the peregrine falcon (*Falco
44 peregrinus*). Peregrines are often seen attacking wader flocks off Griend, making this an ideal model to induce
45 predation risk for knots. Further, drone-based aerial surveys of the island in 2018 (*pers. obs.*) inadvertently
46 revealed that wader flocks actively avoid even slow fixed-wing drones, serving as an initial proof of concept.

47 2 Project description

48 The basic idea is simple: during the 2019 field season (July – October), we propose to investigate the landscape-
49 scale predator avoidance response of knots by subjecting them to controlled predation risk.

50 Flocks of tracked red knots (present among other waders) will be targeted for minimal attack with the
51 drone, i.e., until the entire flock takes off. Rather than examining the effect of a landscape of fear on resource
52 exploitation (as in Bijleveld et al. 2015, see esp. Fig. 2), we will focus for now on examining individual
53 movement responses to predation especially in relation to exploratory personality and prior landscape use (as
54 in Bijleveld et al. 2016).

55 2.1 Project questions

- 56 1. First, we aim to disentangle the relation between predator avoidance and exploration. Is the distance
57 travelled after an attack (relocation distance), and the revisit time to the site of attack, related to the
58 experimental exploration score?
- 59 2. Second, we propose to investigate the effect of predator attacks on social networks. Do attacks disrupt
60 established networks any more than would be expected in the absence of predation?
61 Are post-attack social networks qualitatively different from pre-attack networks, in terms of associations
62 based on exploration scores?
- 63 3. Finally, are there emergent flock-level effects on movement: does the average exploration score of a
64 flock determine the relocation distance after a predator attack?

2.2 Project timeline

The project timeline is strongly dependent on access to the island of Griend, which is owned and managed by Naturmonumenten, and on the availability of the falcon drone. The following must be taken into account:

1. Knot capture and tagging takes place on new moon weeks each month from August to October. Knots are put through behavioural assays over the 2-3 days following capture, and then released. The week following capture is suitable for attacks.
2. A 1 week cooldown period without falcon attacks may be advisable prior to the next catching period, so as not to impact upcoming capture probabilities.
3. The Wadden Sea experiences semi-diurnal tides of 13 hours, meaning that low tide, when knots forage, occurs approximately twice each day. However, except some days when both low tides are during daylight hours, there is only one attack opportunity per day.
4. ATLAS tracking ends in mid- to late-October.

Within these constraints, weeks 36 and 37 (Sept. 02 – Sept. 13; 11 days), and weeks 40, 41, 42 (Sept. 30 – Oct. 18; 19 days) are suitable drone attack periods. Assuming a single attack per low tide, one low tide per day, and 33% unsuitable days ($n \approx 10$), this would result in 20 attacks on knot flocks. Selecting for flocks containing ≥ 10 tracked individuals, we anticipate 150 – 200 predator escape tracks.

In addition, we expect to gain a similar number of tracks from these same individuals on days when they are not subjected to simulated predation. These may be days on which there are either no attacks or when they are not present in the targeted flock.

We propose a dry-run of the project in week 32 (Aug. 5 – 9). This will allow us to investigate whether suitable predator-avoidance tracks can be obtained from tagged waders (NB: sanderlings *C. alba* are tracked from late July, approx. week 31 2019). Further, it will allow the drone pilot and supporting team time to identify and solve issues related to deploying the drone over the mudflats.

References

- Bijleveld, A. I., J. A. van Gils, J. van der Meer, A. Dekinga, C. Kraan, H. W. van der Veer and T. Piersma (2012). Designing a benthic monitoring programme with multiple conflicting objectives. en. In: *Methods in Ecology and Evolution* 3.3, pp. 526–536.
- Bijleveld, A. I., S. Twietmeyer, J. Piechocki, J. A. van Gils and T. Piersma (2015). Natural selection by pulsed predation: survival of the thickest. en. In: *Ecology* 96.7, pp. 1943–1956.
- Bijleveld, A. I., R. B. MacCurdy, Y.-C. Chan, E. Penning, R. M. Gabrielson, J. Cluderay, E. L. Spaulding, A. Dekinga, S. Holthuijsen, J. ten Horn, M. Brugge, J. A. van Gils, D. W. Winkler and T. Piersma (2016). Understanding spatial distributions: negative density-dependence in prey causes predators to trade-off prey quantity with quality. In: *Proceedings of the Royal Society B: Biological Sciences* 283.1828, p. 20151557.
- Carter, A. J., W. E. Feeney, H. H. Marshall, G. Cowlshaw and R. Heinsohn (2013). Animal personality: what are behavioural ecologists measuring? In: *Biological Reviews* 88.2, pp. 465–475.
- Cooke, S. J., S. G. Hinch, M. Wikelski, R. D. Andrews, L. J. Kuchel, T. G. Wolcott and P. J. Butler (2004). Biotelemetry: a mechanistic approach to ecology. In: *Trends in Ecology & Evolution* 19.6, pp. 334–343.

- Kays, R., M. C. Crofoot, W. Jetz and M. Wikelski (2015). Terrestrial animal tracking as an eye on life and planet. en. In: *Science* 348.6240, aaa2478.
- Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith and D. R. MacNulty (2018). Diel predator activity drives a dynamic landscape of fear. en. In: *Ecological Monographs* 88.4, pp. 638–652.
- Lank, D. B., R. W. Butler, J. Ireland and R. C. Ydenberg (2003). Effects of predation danger on migration strategies of sandpipers. en. In: *Oikos* 103.2, pp. 303–319.
- Laundré, J. W., L. Hernández and K. B. Altendorf (2001). Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, U.S.A. In: *Canadian Journal of Zoology* 79.8, pp. 1401–1409.
- Leclerc, M., E. Vander Wal, A. Zedrosser, J. E. Swenson, J. Kindberg and F. Pelletier (2016). Quantifying consistent individual differences in habitat selection. en. In: *Oecologia* 180.3, pp. 697–705.
- Lima, S. L. and L. M. Dill (1990). Behavioral decisions made under the risk of predation: a review and prospectus. In: *Canadian Journal of Zoology* 68.4, pp. 619–640.
- MacCurdy, R., A. Bijleveld, R. Gabrielson, J. Cluderay, E. Spaulding, T. Oudman, J. van Gils, A. Dekinga, T. Piersma and D. Winkler (2015). "Automatic, intensive wildlife radiotracking". en. In: *Untying the Knot*, p. 17.
- Oudman, T., T. Piersma, M. V. Ahmedou Salem, M. E. Feis, A. Dekinga, S. Holthuijsen, J. ten Horn, J. A. van Gils and A. I. Bijleveld (2018). Resource landscapes explain contrasting patterns of aggregation and site fidelity by red knots at two wintering sites. In: *Movement Ecology* 6.1, pp. 24–24.
- Réale, D., S. M. Reader, D. Sol, P. T. McDougall and N. J. Dingemanse (2007). Integrating animal temperament within ecology and evolution. In: *Biological Reviews* 82.2, pp. 291–318.
- Sih, A. and A. M. Bell (2008). "Insights for behavioral ecology from behavioral syndromes". In: *Advances in the Study of Behavior*. Vol. 38. Academic Press, pp. 227–281.
- Sih, A., A. Bell and J. Johnson (2004a). Behavioral syndromes: an ecological and evolutionary overview. In: *Trends in Ecology & Evolution* 19.7, pp. 372–378.
- Sih, A., A. M. Bell, J. C. Johnson and R. E. Ziemba (2004b). Behavioral Syndromes: An Integrative Overview. In: *The Quarterly Review of Biology* 79.3, pp. 241–277.
- Sih, A., J. Cote, M. Evans, S. Fogarty and J. Pruitt (2012). Ecological implications of behavioural syndromes. en. In: *Ecology Letters* 15.3, pp. 278–289.
- Wolf, M. and J. M. McNamara (2012). On the evolution of personalities via frequency-dependent selection. In: *The American Naturalist* 179.6, pp. 679–692.
- Wolf, M. and F. J. Weissing (2010). An explanatory framework for adaptive personality differences. In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 365.1560, pp. 3959–3968.
- Ydenberg, R. C., R. W. Butler, D. B. Lank, B. D. Smith and J. Ireland (2004). Western sandpipers have altered migration tactics as peregrine falcon populations have recovered. In: *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271.1545, pp. 1263–1269.