

Collective Behaviour: Physiology Determines Position

Jens Krause  <https://orcid.org/0000-0002-1289-2857>, Frank Seebacher  <https://orcid.org/0000-0002-2281-9311>

DOI

[10.1016/j.cub.2018.02.070](https://doi.org/10.1016/j.cub.2018.02.070)

Original publication date

23 April 2018 (Available online)

Document version

Accepted manuscript

Published in

Current Biology

Citation

Krause J, Seebacher F. Collective Behaviour: Physiology Determines Position. Curr Biol. 2018;28(8):R351-R4.



Animal Behaviour: Physiology Determines Spatial Positions within Groups

Spatial positions within groups have long been known to affect feeding rates with front positions offering richer pickings. However, positioning behaviour can also be influenced by feeding because big meals reduce the aerobic scope for locomotion, which has important consequences for the organization of group-living animals.

Jens Krause^{1,2*}, and Frank Seebacher³

The costs and benefits of group-living are usually not equally shared between group members and often depend at least partly on the spatial positions individuals occupy within groups. Front positions, for example, provide greater opportunity for feeding [1,2,3], better access to preferred food items, and are indeed the preferred position of hungry individuals [2]. But being at the front of the group has its downsides, because energy expenditure for locomotion is greater [4,5,6], and it increases predation risk [7]. Hence the conventional assumption for fish schools is that hungry individuals adopt front positions where they feed at high rates for a while and then return to central school positions to minimize risk. Individuals are therefore expected to rotate spatial positions depending on their nutritional state, and only take up risky front positions when they need to. A study by McLean et al. [8] sheds new light on the issue of position rotation in groups. Their results show that fish which fed at high rates in front positions eventually have to drop back to central or rear positions because of reduced aerobic scope for locomotion as a result of higher metabolic demands due to food processing (i.e. specific dynamic action). McLean et al.'s study identifies an important physiological correlate of taking up front positions, which was hitherto overlooked in the discussion that focused on how much risk individuals might be willing to take for the reward of higher feeding rates. Animals may be at the front because they will encounter more and better food items. The question now is whether the well-fed fish at the front drop back in position within the school because they are satiated and avoiding risk becomes the dominant motivation or, as Mclean et al. suggest, because they have to drop back because feeding itself reduces the energy available to stay at the front. Fish at the back swim at more or less the same speed as those at the front, but swimming is cheaper at the back because of the hydrodynamic advantage of swimming in other individuals' wake [5]. Mclean et al's work is a nice example of a growing trend to integrate physiological constraints into models of behavioural strategies in a social context [9]. What is particularly elegant in their work is a predictive model, which allows an estimate of how much aerobic scope each fish should have left based on size, amount of food intake, and the time since feeding. This model is an important aspect of the study because it showed that fish with the least aerobic scope available after feeding showed the greatest change in position.

Highly controlled laboratory studies such as the one by Mclean et al. often beg the question of ecological realism because of the artificiality of the conditions and the small group sizes that are investigated. In this context it is satisfying that Mclean et al.'s work recaptured aspects that are known from large schools of pelagic fish in the open ocean [3] which, for example, also showed consistent differences between fish in the time they spent in front positions (with larger fish spending more time up front).

The identification of a physiological constraint also provides an alternative explanation of why animals take up front positions from the conventional view that predation risks are higher in front positions, which does not apply as broadly as previously assumed. Real life – as so often – is considerably more complex. While there is good empirical support for Hamilton's selfish herd model which predicts predation to be higher on the periphery, generalisations to

mobile groups are less well supported. Recent work showed that much depends on the attack strategy of the predator and the avoidance behaviour of the prey groups [10]. In contrast, variation in energetic costs of occupying different spatial positions combined with feeding-induced decreases in aerobic scope provides a promising framework for future work on positioning behaviour of individuals in groups, and it has interesting implications for leadership.

A change of perspective took place in recent years of how leadership is regarded in animal groups. Leaders are not necessarily only those individuals that are dominant, bold and big [11]. Instead, any individual that has relevant information can have a strong influence on the direction of locomotion, thereby facilitating the movement of groups towards food or away from risks [12,13,14,15]. MacLean's work is highly relevant to this debate because it identifies a tendency for consistent differences between individuals to occupy front positions and at the same time highlights that all individuals are subject to certain physiological constraints.

This sets the stage for exciting work in the future. First of all it would be interesting to find out more about what makes individuals different in terms of their positioning behaviour in long-term studies over several days or even weeks. This approach should help to identify characteristics that predispose individuals for leadership positions. Individual fish are known to have unique locomotor characteristics that continue to be present when they move in small groups but gradually disappear as group size increases [16]. Little is known about the causes of such individual variation and its consequences for collective decision-making. Second, long-term experiments would be important to learn more about the time scales at which individuals rotate positions as a result of physiological constraints. In particular, the time course of the specific dynamic action effect is relatively brief. In environments that are not food limited it may be expected that there is a constant rotation of position as fish at the front feed and fall back in position, followed by the next rank of fish feeding and falling back, and so on. Any effects of specific dynamic action could therefore be averaged out over time. The situation would be different if food is limited so that not every individual in the school feeds, or individuals feed on different amounts. In this case, feeding-induced reduction in metabolic scope would have a differential effect on individuals which may have consequences for leadership and group behaviour. Individuals in front positions are known to have a disproportionate influence on movement decisions [17] and long-term experimental studies would allow us to identify the relative contributions that different individuals are likely to make to such decisions. Lastly, an interesting next step from Mclean et al.'s work would be to determine the proportion of aerobic scope that is actually taken up by moving fish. Metabolic rate increases with increasing speed, but the cost of transport, that is the metabolic cost of moving a given distance, decreases with speed at least up to a point [18,19]. Depending on the speed of the school, which may vary with nutritional status and other environmental factors, it may be that aerobic scope becomes more or less limiting.

In conclusion McLean et al.'s study highlights the importance of physiological constraints when it comes to taking up different school positions. Their results suggest that fish eventually abandon front positions not because they want to but because they have to after consuming large meals. These results therefore provide an important alternative to the conventional view of a trade-off between risk and reward for front positions and have important implications for the self-organisation of social systems in terms of leadership.

References

1. O'Connell, C.P. (1972). The interrelationship of biting and filter feeding activity of the northern anchovy (*Engraulis mordax*). J. Fish. Res. Bd. Can. 29, 285-293.
2. Krause, J. (1993). The relationship between foraging and shoal position in a mixed shoal of roach (*Rutilus rutilus*) and chub (*Leuciscus cephalus*): a field study. Oecologia 93, 356-359.
3. DeBlois, E.M., and Rose, G.A (1996). Cross-shoal variability in the feeding habits of migrating Atlantic cod (*Gadus morhua*). Oecologia 108, 192-196.
4. Herskin, J., and Steffensen, J.F. (1998). Energy savings in sea bass swimming in a school: measurements of tail beat frequency and oxygen consumption at different swimming speeds. J. Fish Biol. 53, 366-376.
5. Killen, S.S., Marras, S., Steffensen, J.F. & McKenzie, D.J. (2012). Aerobic capacity influences the spatial position of individuals within fish schools. Proc. Roy. Soc. Biol. Lond. B 279, 357–364.
6. Voelkl, B., Portugal, S.J., Unsölde, M., Usherwood, J.R., Wilson, A.M., and Johannes, F. (2015). Matching times of leading and following suggest cooperation through direct reciprocity during V-formation flight in ibis. PNAS 112, 2115–2120.
7. Bumann, D., Krause, J., and Rubenstein, D.I. (1997). Mortality risk of spatial positions in animal groups: the danger of being in the front. Behaviour 134, 1063-1076.
8. McLean, S., Persson, A., Norin T, and Killen S.S. 2018. Metabolic costs of feeding predictively alter the spatial distribution of individuals in fish schools. Curr. Biol.
9. Seebacher, F., and Krause, J. (2017). Physiological mechanisms underlying animal grouping behaviour. Phil. Trans. Roy. Soc. B 372, 1727.
10. Ward, A.J.W., and Webster, M. (2016). Sociality: The behaviour of group-living animals. Springer, Heidelberg & New York.
11. King, A.J., Johnson, D.D.P., and Van Vugt, M. (2009). The origins and evolution of leadership. Curr. Biol. 19, 911-916.
12. Grünbaum, D. (1998). Schooling as a strategy for taxis in a noisy environment. Evol. Ecol. 12, 503-522.
13. Ward, A.J.W., Sumpter, D.J.T., Couzin, I.D., Hart, P.J.B., and Krause, J. (2008). Quorum decision-making facilitates information transfer in fish shoals. PNAS 105, 6948-6953.
14. Couzin, I.D., Ioannou, C.C., Demirel, G., Gross, T., Torney, C.J., Hartnett, A., Conradt, L., Levin, S.A., and Leonard, N.E. (2011). Uninformed individuals promote democratic consensus in animal groups. Science 334, 1578-1580.

15. Berdahl, A., Torney, C.J., Ioannou, C.C., Faria, J.J., and Couzin, I.D. (2013). Emergent sensing of complex environments by mobile animal groups. *Science* 339, 574-576.
16. Herbert-Read, J.E., Krause, S., Morrell, L.J., Schaerf, T.M., Krause, J., and Ward, A.J.W. (2013). The role of individuality in collective group movement. *Proc. Roy. Soc. Lond. B* 280, 20122564.
17. Katz, Y., K Tunstrøm, K., Ioannou, C.C., Huepe, C., and Couzin, I.D. (2011). Inferring the structure and dynamics of interactions in schooling fish. *PNAS* 108, 18720-18725.
18. Claireaux, G., Couturier, C., Groison, A.-L. (2006). Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (*Dicentrarchus labrax*). *J. Exp. Biol.* 209, 3420-3428.
19. Seebacher, F., Borg, J., Schlotfeldt, K., and Yan, Z. (2016). Energetic cost determines voluntary speed only in familiar environments. *J. Exp. Biol.* 219, 1625-1631.

¹Humboldt University, Faculty of Life Sciences, 10115 Berlin, Germany;

²Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany.

*Email: j.krause@igb-berlin.de

³School of Biological Sciences A08, University of Sydney, NSW 2006 Australia.