Acknowledgments

The author group is part of the Tansley Working Groups initiative sponsored by the UK Natural Environment Research Council (NERC) (http://www.nerc.ac.uk/). T.H.O. was supported by the Wessex Biodiversity Ecosystem Services Sustainability (BESS) project (ref. NE/J014680/1) within the NERC BESS Programme. V.P. was supported by Fundação para a Ciência e a Tecnologia (BPD/80726/2011). Contributions of O.L.P. were supported by the University of Zurich Research Priority Program on 'Global Change and Biodiversity' and SNSF Project 31003A_137921 'Predicting Community Responses to Environmental Change'.

Supplemental Information

Supplemental data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.tree.2015.12.008.

[1]School of Biological Sciences, University of Reading, Reading RG6 6AS, UK
[2]NERC Centre for Ecology and Hydrology, Wallingford, UK
[3]Joint Nature Conservation Committee, UK
[4]University of Southampton, Southampton, UK
[5]University of Sheffield, Sheffield, UK
[6]Department of Plant Sciences, University of Oxford, Oxford, UK
[7]Imperial College London, London, UK
[8]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland
[9]Instituto Superior Técnico, University of Lisbon, Lisbon, Portugal
[10]University of York, York, UK
[11]Department of Earth and Planetary Science, University of California, Berkeley, CA, USA
[12]University College London, London, UK
[13]Faculty of Sustainability, Institute of Ethics and Transdisciplinary Sustainability Research, Leuphana University of Lüneburg, Lüneburg, Germany

*Correspondence: t.oliver@reading.ac.uk (T.H. Oliver).
http://dx.doi.org/10.1016/j.tree.2015.12.008

References

1. Mori, A.S. (2016) Resilience in the studies of biodiversity-ecosystem functioning. *Trends Ecol. Evol.* 31, 87–89
2. Nimmo, D.G. *et al.* (2015) *Vive la résistance*: reviving resistance for 21st century conservation. *Trends Ecol. Evol.* 30, 516–523
3. Oliver, T.H. *et al.* (2015) Biodiversity and the resilience of ecosystem services. *Trends Ecol. Evol.* 30, 673–684
4. Gunderson, L. *et al.* (2010) *Foundations of Ecological Resilience,* Island Press
5. Newton, A. and Cantarello, E. (2015) Restoration of forest resilience: an achievable goal? *New Forests* 46, 645–668
6. Loreau, M. and de Mazancourt, C. (2013) Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecol. Lett.* 16, 106–115
7. Pasari, J.R. *et al.* (2013) Several scales of biodiversity affect ecosystem multifunctionality. *Proc. Natl. Acad. Sci. U.S.A.* 110, 10219–10222
8. Reiss, J. *et al.* (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* 24, 505–514
9. Karp, D.S. *et al.* (2011) Resilience and stability in bird guilds across tropical countryside. *Proc. Natl. Acad. Sci. U.S.A.* 108, 21134–21139
10. Dai, L. *et al.* (2012) Generic indicators for loss of resilience before a tipping point leading to population collapse. *Science* 336, 1175–1177
11. Grimm, V. and Wissel, C. (1997) Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. *Oecologia* 109, 323–334
12. Truchy, A. *et al.* (2015) Linking biodiversity, ecosystem functioning and services, and ecological resilience: towards an integrative framework for improved management. *Adv. Ecol. Res.* Published online November 26, 2015. http://dx.doi.org/10.1016/bs.aecr.2015.09.004

Letter

Consumptive Tourism Causes Timidity, Rather Than Boldness, Syndromes: A Response to Geffroy *et al.*

Robert Arlinghaus,[1,2,*,@] Josep Alós,[1] Thomas Klefoth,[3] Kate Laskowski,[1] Christopher T. Monk,[1] Shinnosuke Nakayama,[1,2] and Arne Schröder[1]

Geffroy *et al.* [1] proposed that nature-based tourism reduces the fearfulness and antipredator behavior of animals, leading towards a boldness syndrome that elevates natural predation rates and could trigger cascading effects on populations and communities. We agree with the framework, hypotheses, and future research needs proposed in [1], but they apply strictly to nonthreatening human–wildlife interactions. However, nature-based tourism is often consumptive, where wild-living animals are chased, stressed, and eventually harvested in activities such as recreational fishing and hunting. No threatening forms of human use of animals were elaborated in [1]. As a complementary perspective, we here propose that consumptive nature-based tourism might lead to opposite behavioral outcomes to those proposed in [1] by inducing a timidity, rather than a boldness, syndrome (Figure 1).

Human exploitation of wild-living animals creates a 'landscape of fear' [2,3]. A commonly reported plastic behavioral response of animals to human-induced predation risk involves increased antipredator behavior and heightened timidity, characterized by a greater use of refuges and reduced activity [2–8]. For such effects to happen, the experience of nonlethal, yet threatening stimuli caused by humans are often sufficient. For example, catch-and-release angling is increasingly common in tourism-based fishing operations. Being hooked, physiologically stressed, and eventually released promotes refuge-seeking behaviors that reduce vulnerability to fishing, which may also affect nonhooked conspecifics through social learning [8,9]. In addition to plastic effects within the behavioral reaction norm, lethal consumptive tourism may also cause evolutionary responses in a range of life-history and behavioural traits that collectively increase the average timidity levels of surviving individuals [3,6,7,10–12]. For example, bold, explorative, aggressive, and active behavioral types (aka 'personalities') within exploited wildlife populations are often selectively harvested [3,7,10–12]. The positive heritability characterizing most personality traits in turn could facilitate an evolutionary (i.e., genetic) response of timidity-related behaviors [6,7,12]. Increased timidity due to learning and/or evolutionary adaptation can occur in both predator and prey populations when they are exposed to threatening stimuli by recreational fishers or hunters. The net result for a prey species should generally involve a reduction, rather than an increase [1], in natural mortality risk because either the prey becomes shyer when they are exploited or it benefits from an increased timidity of the exploited predator, thereby being

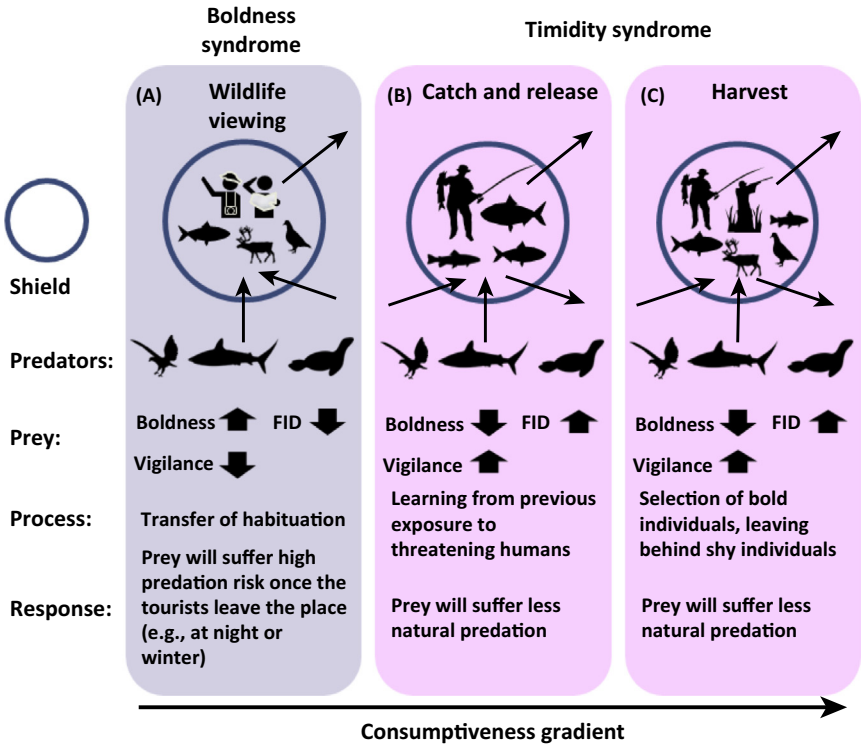

Figure 1. Animals Respond to Human Presence Along a Gradient of Consumptiveness from Entirely Nonconsumptive Nature-Based Tourism to Harvesting-Based Exploitation (from Left to Right). When nonconsumptive and consumptive humans interact with wild animals, they create a temporal shield with different responses, including habituation (A) and fear of humans (B,C). (A) The original boldness syndrome introduced by [1]. The arrows represent the fluxes in-and-out of the prey organisms, once the humans leave the shield and the predators come in. In (A), a temporal shield between humans and animals is expected to induce higher boldness in the animals as a result of habituation to humans. When the humans leave the shield and predators enter, the prey is expected to be more vulnerable to natural predators as predicted by [1]. (B,C) The timidity syndrome introduced here. (B) A nonharvest shield that emerges when fishes exposed to catch-and-release fishing or wildlife exposed to hunting induce fear and antipredator behavior. The mechanism here is focused on learning in response to previous capture-and-release experiences or experience of shooting, possibly aggravated by social information flow. The flux of animals to the shield should be unidirectional because the animal density should remain fairly constant due to the lack of harvest. However, the fear of consumptive humans may in the long run also induce a migration outside of the shield if animals move into refuges, which might attract novel bold and explorative individuals to the shield, restarting the cycle. (C) The case when humans chase and harvest wild animals, where surviving individuals are bound to become shyer, increase their fearfulness and flight initiation distance (FID) in response to the behavioral-mediated selective process and through learning by private or public information. The surviving individuals then characterize a lower encounter probability not only with humans, but also in relation to natural predators, creating a temporal shield through a timidity syndrome. Animals might leave the shield to avoid the risk of death imposed by hunting or fishing, similar to (B), while naive bold and highly explorative individuals may occasionally enter from outside the shield because harvesting relaxes the density-dependent food competition and, hence, attracts migrants. The newcomers may then also be selectively harvested or plastically respond to the human predation risk. Similar to (A), fishers or hunters may also leave the shield in (B,C) due to seasonal patterns of exploitation, including holiday patterns, or because of constraints imposed by policy (e.g., a seasonal closure or a protected area). This would attract predators to the shields during the absence of humans, but prey might be less vulnerable to predation. Modified from [1] (A).

released from predation risk. However, in catch-and-release angling, released individuals might also suffer from immediate predation before even reaching refuges due to physical exhaustion and short-term behavioral alterations caused by stress.

The timidity syndrome proposed here in response to consumptive tourism not only predicts reduced natural mortality risks in prey organisms, but also implicates several other ecological and managerial consequences for social groups, populations, food webs, ecological services, and assessment of stocks. For example, animal groups might systematically lose keystone individuals and then show reduced ecological performance, such as during spawning migrations, where the leadership by old, experienced animals may be particularly important. Moreover, trophic relations are bound to be altered when hunted and fished animals are forced into refuges and away from profitable foraging sites. Thus, the timidity syndrome may moderate the degree of bottom-up or top-down control of food webs depending on the exact geographical configuration of foraging and refuge sites in an ecosystem [2]. Finally, from a social and economic perspective, increased ability to avoid capture (a key component and indicator of the timidity syndrome that we propose [5–9]) may not only lower the satisfaction of anglers and hunters by reducing catch rates or sightings, but also contribute to systematic erosion of the quality of user-dependent monitoring data as a surrogate of stock abundance due to hyperdepletion effects where catch rates or sightings decline more strongly than underlying abundance [6]. Reduced exposure to fish and wildlife due to increased timidity may also foster a belief among tourists that there is less wildlife or fewer fish than desired, which either threatens the economic operation by reducing demand or increases stakeholder conflicts.

Similar to the boldness syndrome [1], one of the most important outstanding questions in relation to the timidity syndrome is investigating whether the reduced exposure to fishing gear or hunters observed in heavily exploited stocks also alters the natural behavior of the exploited species in relation to natural predators. If fish and wildlife only selectively responded to human threat signals in the short term, the ecological and food-web effects of

the timidity syndrome could be small and only socioeconomic impacts would be prominent. To sort this and other pertinent questions out, improved collaboration among field behavioral ecologists, fisheries and wildlife biologists, managers, and tourism operators is needed to investigate the propositions introduced here (Figure 1) and in [1]. Answering these questions is certainly not only of academic appeal, but also of large importance to fish and wildlife management as well as tourism.

Acknowledgments

This work was funded by the B-Types grant (Gottfried-Wilhelm-Leibniz-Community, grant no. SAW-2013-IGB-2) to R.A. and two Marie Curie Post Doc grants to J.A. (Fish & Fishers, grant No. 327160) and A.S. (BT-LH-Link, grant no. 660643).

[1]Department of Biology and Ecology of Fishes, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany
[2]Division of Integrative Fisheries Management, Department of Crop and Animal Sciences, Faculty of Life Sciences, Humboldt-Universität zu Berlin, Invalidenstrasse 42, 10115 Berlin, Germany
[3]State Sportfisher Association of Lower Saxony, Bürgermeister-Stümpel-Weg 1, 30457 Hannover, Germany

*Correspondence: arlinghaus@igb-berlin.de (R. Arlinghaus).
@Twitter: @RArlinghausFish

http://dx.doi.org/10.1016/j.tree.2015.11.008

References

1. Geffroy, B. *et al.* (2015) How nature-based tourism might increase prey vulnerability to predators. *Trends Ecol. Evol.* 30, 755–765
2. Laundré, J.W. *et al.* (2014) The landscape of fear: the missing link to understand top-down and bottom-up controls of prey abundance? *Ecology* 95, 1141–1152
3. Ciuti, S. *et al.* (2012) Human selection of elk behavioural traits in a landscape of fear. *Proc. Roy. Soc. B* 279, 4407–4416
4. Lone, K. *et al.* (2015) An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Anim. Behav.* 102, 127–138
5. Januchowski-Hartley, F.A. *et al.* (2015) Local fishing influences coral reef fish behavior inside protected areas of the Indo-Pacific. *Biol. Conserv.* 182, 8–12
6. Alós, J. *et al.* (2015) Recreational angling intensity correlates with alteration of vulnerability to fishing in a carnivorous coastal fish species. *Can. J. Fish. Aquat. Sci.* 72, 217–225
7. Tsuboi, J. *et al.* (2015) Behaviour-mediated alteration of positively size-dependent vulnerability to angling in response to historical fishing pressure in a freshwater salmonid. *Can. J. Fish. Aquat. Sci.* Published online October 6, 2015. http://dx.doi.org/10.1139/cjfas-2014-0571
8. Klefoth, T. *et al.* (2011) Behavioural and fitness consequences of direct and indirect non-lethal disturbances in a catch-and-release northern pike (*Esox lucius*) fishery. *Know. Manage. Aquat. Ecosyst.* 403, 11
9. Askey, P.J. *et al.* (2006) Linking angling quality and learning under catch and release regulations: why are the fish not biting? *N. Am. J. Fish. Manage.* 26, 1020–1029
10. Biro, P.A. and Post, J.R. (2008) Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proc. Natl. Acad. Sci. U.S.A.* 105, 2919–2922
11. Härkönen, L. *et al.* (2014) Explorative behavior increases vulnerability to angling in hatchery-reared brown trout *Salmo trutta*. *Can. J. Fish. Aquat. Sci.* 71, 1900–1909
12. Sutter, D.A.H. *et al.* (2012) Recreational fishing selectively captures individuals with the highest fitness potential. *Proc. Natl. Acad. Sci. U.S.A.* 109, 20960–20965

Letter

In Defense of the Ecotourism Shield: A Response to Geffroy *et al.*

Lee A. Fitzgerald[1,*] and Amanda L. Stronza[2]

Geffroy *et al.* [1] pose a bold scenario: nature tourists and ecotourists may create a 'human shield' in some circumstances, but ultimately tourism habituates animals and makes them susceptible to poaching and predation. In short, tourism is harmful to wildlife. The authors state that these problems from tourism can extend across entire populations of species and they suggest that tourism can even select for increased predation risk and drive loss of genetic diversity. We argue that these ideas are speculative and merit more careful analysis. We write with some urgency to critique the arguments and highlight the fallacies. We echo the authors' call for rigorous studies 'in the wild with real predators' and hope the paper will inspire many. In the meantime, asserting that nature tourism and ecotourism may be harmful to animals is premature and problematic. It sends a countervailing, mixed message to conservation stakeholders about the real importance of tourism for protecting wildlife, both in protected areas and in surrounding communities [2].

The shield of ecotourism extends across areas greater than the places where tourists interact with wildlife. When designed to provide benefits to conservation and local communities, ecotourism, sustainable tourism, and other forms of nature tourism help generate revenues and political support while also creating direct incentives to protect wildlife, ecosystems, and landscapes. The very foundation of the world's first national parks in the USA, and countless protected areas around the world, has been tourism. Tourism creates a large umbrella that is necessary for wildlife conservation and protection of large landscapes. Tourism helps fund programs for local villagers, who act as gatekeepers against poachers [3]. In Botswana, safari operators are leading efforts to reintroduce rhinos, bringing them in from areas where poaching is escalating. These animals are not habituated and most may never see an ecotourist [4]. Tourism has led to reduced hunting and transitioning from hunting to guiding, from direct, consumptive uses of biodiversity to indirect, less consumptive uses [5]. Buckley [3] noted that 'for over half of the red-listed mammal species at least five percent rely on tourism revenue to survive. For one in five – including rhinos, lions, and elephants – that rises to at least 15 percent of individuals. Simply put, if tourism money is cut abruptly, poaching will increase' [3].

The Geffroy *et al.* [1] model hinges on the transfer of habituation to the suite of predators in nature. To date, there is no conclusive evidence. The study on fox squirrels [6] cited as the most compelling showed that at one university and in suburban parks fox squirrels were less responsive to recordings of red-tailed hawks and coyotes. Because coyotes and hawks are scarce at the campus and parks, that study could not distinguish between transfer of habituation and low predation risk. Another study [7] found that in dik-diks habituation did not transfer to jackals. Likewise, predation on domestic cattle is an unconvincing example of how wildlife can become susceptible when habituated. The salient message from that