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Harvesting as a potential selective pressure on behavioral traits

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Running head: Behavioral harvest-induced selection

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Summary

1. Human activities are a major evolutionary force affecting wild populations. Selective pressure from harvest has mainly been documented for life-history and morphological traits. The probability for an individual to be harvested, however, may also depend on its behavior.

2. We report empirical studies that examined whether harvesting can exert selective pressures on behavioral traits.

3. We show that harvest-induced selection on behavioral traits is not specific to a particular harvest method and can occur throughout the animal kingdom.

4. *Synthesis and applications.* Managers need to recognize that artificial selection is possible. More empirical studies integrating physiological, behavioral, and life-history traits should be carried out to test specific predictions of the potential for harvest-induced selection on heritable traits using models developed in fisheries. To limit selective pressure on behavior imposed by harvesting, managers could reduce harvest quotas or vary harvest regulations over time and/or space to reduce the strength of selection on a particular phenotype.

Keywords: angling, evolutionary consequences, exploitation, fisheries, gillnet, harvest-induced selection, hunting, passive and active gear, vulnerability.

Introduction

Humans are considered as one of the major selective forces shaping traits of species (Palumbi 2001) and may cause faster phenotypic changes than many natural drivers (Hendry, Farrugia & Kinnison 2008; Darimont *et al.* 2009). Phenotypic changes are particularly drastic when humans act as predators and harvest wild populations (Darimont *et al.* 2009). Harvesting can induce selective pressures on wild animal populations by increasing mortality and by non-random removal of specific phenotypes. Harvesting has been shown to induce selective pressure in several species (Allendorf *et al.* 2008) that may ultimately result in evolutionary responses (Jørgensen *et al.* 2007; Pigeon *et al.* 2016).

Selective pressure caused by human harvest, hereafter referred to as harvest-induced selection, has mostly been documented for life-history and morphological traits and can be caused by size-selective harvesting. For example, trophy hunting of male bighorn sheep (*Ovis canadensis*) selected for smaller horn size (Coltman *et al.* 2003; Pigeon *et al.* 2016), and size-selective fishing affected the evolution of life histories in zebra fish (*Danio rerio*) (Uusi-Heikkilä *et al.* 2015). In size-selective harvesting, typically a specific phenotype is targeted leading to harvest-induced selection. Harvest-induced selection on behavioral traits, however, can be due to behavioral differences between individuals affecting their probability of being harvested (Uusi-Heikkilä *et al.* 2008; Heino & Godø 2002). This pattern was observed in behavioral studies showing that the probability of capturing or sampling (for scientific research instead of harvesting) a specific individual in a population could be biased due to consistent individual differences in behavior, i.e., animal personality (Biro & Dingemanse 2009; Carter *et al.* 2012; Biro 2013). These individual behavioral differences are often heritable (Postma 2014; Dochtermann, Schwab & Sih 2015). Humans can therefore, consciously or not, modulate the evolution of animal behavior by removing (harvesting) or reproducing (breeding) specific individuals within a population (Price 1984). Although important for wildlife management and conservation, much less attention has been devoted to harvest-induced selection on behavioral traits compared to life-history or morphological traits (Uusi-Heikkilä *et al.* 2008; Heino, Díaz Pauli & Dieckmann 2015) and to whether this selection may lead to evolution of behaviors that are different from those favored by natural selection (e.g., Olsen & Moland (2011) for morphological traits).

Harvesting as a selective pressure on behavioral traits

Most of the theoretical work and predictions for behavioral harvest-induced selection are derived from the fisheries literature. Arlinghaus *et al.* (2016) suggested that harvest should select for shyer and more vigilant individuals. In fisheries, predictions made on harvest-induced selection often depend on the gear type used, and Alós, Palmer & Arlinghaus (2012) predicted that passive gear should select for individuals with lower activity levels. In sport hunting, a hunter must see an individual of the species of interest before she/he can select a target animal based on a morphological trait or a sex/age class. Therefore, we hypothesize that behavioral traits that increase vulnerability or visibility, such as selection of open areas, more active individuals during hunting hours, or boldness, should have a strong effect on the probability that an individual will present itself as a possible target.

Here we report studies where harvest-induced selection of behavioral traits was clearly investigated. We searched the scientific literature database Scopus® for peer-reviewed papers using different combinations of the following seven keywords: harvesting, hunting, fisheries, behavior, vulnerability, exploitation, and selective pressure. The literature contains numerous studies on the immediate effects of harvesting on behavior (i.e., plastic response or “learning”) [e.g., Raat (1985), Ordiz *et al.* (2012)] or studies showing behavioral differences between high and low vulnerability fish strains [e.g. Nannini *et al.* (2011), Sutter *et al.* (2012)], or studies showing behavioral differences between fish caught with different methods or lures [e.g. Wilson *et al.* (2015)], which suggests that harvesting might induce a selective pressure on behaviors. Here, however, we only retained studies that directly examined whether harvesting acted as a selective pressure on behavioral traits. The limited amount of literature examining harvest-induced selection on behavior likely reflects the difficulties in collecting quantitative information on behavioral traits expressed by harvested and non-harvested individuals necessary to investigate behavioral harvest-induced selection. This is particularly true for fish, because it is rarely possible to make observations on fish that are not captured (Härkönen *et al.* (2016), but see Olsen *et al.* (2012)), and longitudinal behavioral time-series data from wild populations hardly exist (Jørgensen & Holt 2013). We categorized the 13 retained studies in two groups: experimental studies in the laboratory or natural conditions, and observational studies in the wild.

Experimental studies

We found seven experimental studies showing that harvest can act as a selective pressure on behavioral traits (Table 1; but see Vainikka, Tammela & Hyvärinen (2016)). From the seven studies showing harvest-induced selection of behavioral traits, six were conducted in fishes and one in a crustacean. Angling removed more vulnerable individuals in largemouth bass (*Micropterus salmoides*) (Philipp *et al.* 2009) and common carp (*Cyprinus carpio*) (Klefoth, Pieterek & Arlinghaus 2013), while traps removed bolder guppies (*Poecilia reticulata*) and common yabby (*Cherax destructor*) (Biro & Sampson 2015; Diaz Pauli *et al.* 2015). Trawling removed shyer guppies (Diaz Pauli *et al.* 2015) and minnows (*Phoxinus phoxinus*) with lower swim speed (Killen, Nati & Suski 2015). These studies suggest that harvesting can act as a selective pressure on a behavioral trait and that passive gear should select against boldness and more explorative individuals, while active gear should select against shyness, and angling selects against more aggressive, bold, and vulnerable individuals (Heino & Godø 2002; Arlinghaus *et al.* 2016). Harvest-induced selection patterns obtained in laboratory experiments appear to be consistent with experiments in natural settings (Biro & Post 2008), suggesting that harvesting can act as a selective pressure in the wild.

Observational studies

We found six studies showing harvest-induced selection on different behavioral traits in the wild, ranging from the timing of migration to boldness and defensiveness (Table 1). These studies involved fishes, snakes, birds, and mammals in Japan, Norway, United Kingdom, Canada, and the USA. Similarly to experimental studies, observational studies showed that harvest-induced selection was caused by different harvest methods (shotgun, rifle hunting, passive gear, angling), and that behavioral traits under selection may vary in relation to the harvest method used (Table 1). In sockeye salmon (*Oncorhynchus nerka*) harvesting selected against individuals that migrated later in the season in a population where exploitation rates vary systematically over the course of the fishing season (Quinn *et al.* 2007). In this population, migration timing became earlier over the years (Quinn *et al.* 2007). Such temporal behavioral changes could be caused by environmental factors, but could also be, at least partly, a response to harvest-induced selection if migration timing is heritable (Quinn *et al.* 2007).

Consequences of behavioral harvest-induced selection

Behavioral traits under harvest-induced selection can only evolve if they are heritable (Postma 2014; Dochtermann, Schwab & Sih 2015). In addition to the changes in migration timing of sockeye salmon discussed above (Quinn *et al.* 2007), two studies suggested that harvest might have been important in the evolution of a genetic locus related to habitat use of Atlantic cod (*Gadus morhua*) in Iceland (Árnason, Hernandez & Kristinsson 2009; Jakobsdottir *et al.* 2011). However, we found no observational studies that could unequivocally show evolution in behavior caused by harvesting. Absence of evidence for harvest-induced evolution of behavioral traits in the wild, however, does not imply that such evolution is unlikely or uncommon. Instead, it may reflect the difficulties to obtain the necessary longitudinal data on behaviors in harvested populations (Clutton-Brock & Sheldon 2010; Jørgensen & Holt 2013). Even when adequate data are available, it remains challenging to show that harvest is the driver of evolutionary change and to disentangle phenotypic plasticity from genetic change (Merilä & Hendry 2014). Although it has not been documented in the wild, evolutionary changes in behavioral traits due to harvest have been shown in experimental studies (Philipp *et al.* 2009). Laboratory experiments are useful to evaluate the potential for harvest-induced selection and evolutionary response in behavioral traits, but extrapolation of results to natural systems are difficult, as some relationships observed in the laboratory might not persist in the wild (Wilson *et al.* 2011).

Conclusions

Humans have harvested wild species for millennia and human evolution is strongly linked with harvesting. However, technological developments have increased our efficiency to harvest, with many consequences (Milner, Nilsen & Andreassen 2007; Fenberg & Roy 2008; Allendorf *et al.* 2008). Morphological, life-history, and behavioral traits form the phenotype of an individual and thus affect its vulnerability to harvest (Uusi-Heikkilä *et al.* 2008). There is increasing evidence that behavioral traits are correlated with physiological and life-history traits (Biro & Stamps 2008; Réale *et al.* 2010). Therefore, even if harvesting specifically targets a behavioral trait, changes in life-history, morphological, and/or physiological traits can be observed. For example, changes in behaviors were observed due to size-selective harvesting in zebra fish (Uusi-Heikkilä *et al.* 2015), and size-selective harvesting of Atlantic silverside (*Menidia menidia*) resulted in lower larval growth rate, food consumption rate and conversion efficiency, and vertebrae number (Walsh *et al.* 2006; Duffy *et al.* 2013). If individuals with certain life-history, morphological and behavioral phenotypes are heavily harvested, selection may quickly lead to the evolution of a population with a lower harvest yield (Conover & Munch 2002), because this population will now mostly be composed of individuals with lower growth rate (Conover & Munch 2002; Biro & Sampson 2015) that are also more difficult to harvest (Philipp *et al.* 2009). In many cases, selective pressures imposed by harvesting oppose natural selection (Conover 2007; Olsen & Moland 2011). While some traits can genetically recover after harvest-induced selection ceases (Conover, Munch & Arnott 2009), some traits may not (Salinas *et al.* 2012; Pigeon *et al.* 2016), which can impair population recovery after harvest has ceased (Laugen *et al.* 2014).

Recommendations

Even though behaviors are often easier to observe and quantify in terrestrial ecosystems, most of the literature and predictions on behavioral harvest-induced selection come from fisheries. Despite differences in the harvest methods used in fisheries and hunting, behavioral data from terrestrial harvested populations can be complementary to fisheries data and could offer an opportunity to test predictions developed for fisheries in terrestrial ecosystems. For example, predictions made for passive gear in fisheries could be applied to “still hunting” or “bait hunting”, but might not be appropriate for “stalking”. Therefore, we suggest a synergistic approach and recommend to increase discussions and collaborations between researchers studying harvest-induced selection in fisheries and terrestrial ecosystems.

Integrating genetic and evolutionary effects of harvesting into management and conservation is central for achieving sustainable harvesting (Conover & Munch 2002; Allendorf *et al.* 2008). Acknowledging that harvest is selective by nature is the first step toward that goal. Even if harvest is random regarding phenotypes, it increases mortality and therefore selects for faster growing and earlier reproducing individuals ("*r*" life-history strategy) rather than slow growing and late reproducing individuals ("*K*" life-history strategy) (Pianka 1970). Ideally, in harvested populations, monitoring programs should be introduced to detect and monitor potential harvest-induced selection and its consequences. Such programs would require longitudinal data on multiple phenotypic traits, including behavioral traits, of harvested and non-harvested individuals in the population. This would allow evaluating the direction and strength of harvest-induced selection in comparison to natural selection. When required, different mitigation measures could be implemented in management plans to reduce the impacts of harvest-induced selection. For example, reducing harvest quotas should reduce the strength of selection or managers could establish harvest regimes that mimic natural selection (Milner, Nilsen & Andreassen 2007).

Such monitoring programs are challenging tasks requiring a considerable amount of time and money. In the meantime, we suggest using a precautionary approach when harvesting natural populations. Harvest quotas should not be based on maximum yield but rather aim at preserving natural variation shaped by natural selection (Fenberg & Roy 2008). We suggest, based on our results, to vary harvest regulations (e.g. based on sex, age, or phenotypes harvested and harvest methods used) spatio-temporally to reduce the strength of selection on a particular phenotype.

Authors' Contributions

All authors conceived the idea; ML made de literature search and the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Table 1. Examples of experimental and observational studies showing that harvest can act as a selective pressure on behavior.

Species	**Harvest method**	**Trait**	**Direction of the selective effect** **Harvest selects against individual that are:**	**Reference**
Experimental study in the laboratory or in natural conditions				
Poecilia reticulata	Trap	Bold–Shy	Bolder	Diaz Pauli *et al.* 2015
	Trawl	Bold–Shy	Shyer	Diaz Pauli *et al.* 2015
Phoxinus phoxinus	Trawl	Swim speed	Slower	Killen, Nati & Suski 2015
Salmo trutta	Fly-fishing	Exploration	More explorative	Härkönen *et al.* 2014
Cyprinus carpio	Angling	Vulnerability	More vulnerable	Klefoth, Pieterek & Arlinghaus 2013
Micropterus salmoides	Angling	Vulnerability	More vulnerable	Philipp *et al.* 2009
Oncorhynchus mykiss	Gillnet	Bold/Shy–Fast/Slow	Faster-bolder	Biro & Post 2008
Cherax destructor	Trap	Bold–Shy	Bolder	Biro & Sampson 2015
Observational study				
Oncorhynchus nerka	Angling	Migration timing	Migrated later in season	Quinn *et al.* 2007
Gadus morhua	Passive gear	Habitat use	Use more shallow-water	Olsen *et al.* 2012
	Passive gear	Vertical migration	Have a strong diel vertical migration	Olsen *et al.* 2012
	Passive gear	Horizontal movement	Have a predictable movement pattern	Olsen *et al.* 2012
Gloydius blomhoffii	Not mentioned	Flight distance	Have lower flight distance	Sasaki *et al.* 2009
	Not mentioned	Defensiveness	More defensive	Sasaki *et al.* 2009

Phasianus colchicus	Shotgun hunting	Bold–Shy	Bolder	Madden & Whiteside 2014
Cervus elaphus	Rifle hunting	Habitat use	Use habitat with less concealing cover	Lone *et al.* 2015
	Rifle hunting	Habitat use	Use open areas	Ciuti *et al.* 2012
	Rifle hunting	Habitat use	Closer to roads and use flatter terrain	Ciuti *et al.* 2012
	Rifle hunting	Movement rate	Have higher movement rate	Ciuti *et al.* 2012

References

Allendorf, F.W., England, P.R., Luikart, G., Ritchie, P.A. & Ryman, N. (2008) Genetic effects of harvest on wild animal populations. *Trends in Ecology & Evolution*, **23**, 327–337.

Alós, J., Palmer, M. & Arlinghaus, R. (2012) Consistent selection towards low activity phenotypes when catchability depends on encounters among human predators and fish. *PLoS ONE*, **7**, e48030.

Arlinghaus, R., Alós, J., Klefoth, T., Laskowski, K., Monk, C.T., Nakayama, S. & Schröder, A. (2016) Consumptive tourism causes timidity, rather than boldness, syndromes: A response to Geffroy et al. *Trends in Ecology & Evolution*, **31**, 92–94.

Árnason, E., Hernandez, U.B. & Kristinsson, K. (2009) Intense habitat-specific fisheries-induced selection at the molecular Pan I locus predicts imminent collapse of a major cod fishery. *PLoS ONE*, **4**, e5529.

Biro, P.A. (2013) Are most samples of animals systematically biased? Consistent individual trait differences bias samples despite random sampling. *Oecologia*, **171**, 339–345.

Biro, P.A. & Dingemanse, N.J. (2009) Sampling bias resulting from animal personality. *Trends in Ecology & Evolution*, **24**, 66–67.

Biro, P.A. & Post, J.R. (2008) Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 2919–2922.

Biro, P.A. & Sampson, P. (2015) Fishing directly selects on growth rate via behaviour : implications of growth-selection that is independent of size. *Proceedings of the*

Royal Society B, **282**, 20142283.

Biro, P.A. & Stamps, J.A. (2008) Are animal personality traits linked to life-history productivity? *Trends in Ecology & Evolution*, **23**, 361–368.

Carter, A.J., Heinsohn, R., Goldizen, A.W. & Biro, P.A. (2012) Boldness, trappability and sampling bias in wild lizards. *Animal Behaviour*, **83**, 1051–1058.

Ciuti, S., Muhly, T.B., Paton, D.G., McDevitt, A.D., Musiani, M. & Boyce, M.S. (2012) Human selection of elk behavioural traits in a landscape of fear. *Proceedings of the Royal Society B*, **279**, 4407–4416.

Clutton-Brock, T. & Sheldon, B.C. (2010) Individuals and populations: the role of long-term, individual-based studies of animals in ecology and evolutionary biology. *Trends in Ecology & Evolution*, **25**, 562–573.

Coltman, D.W., O'Donoghue, P., Jorgenson, J.T., Hogg, J.T., Strobeck, C. & Festa-Bianchet, M. (2003) Undesirable evolutionary consequences of trophy hunting. *Nature*, **426**, 655–658.

Conover, D.O. (2007) Nets versus nature. *Nature*, **450**, 179–180.

Conover, D.O. & Munch, S.B. (2002) Sustaining fisheries yields over evolutionary time scales. *Science*, **297**, 94–96.

Conover, D.O., Munch, S.B. & Arnott, S.A. (2009) Reversal of evolutionary downsizing caused by selective harvest of large fish. *Proceedings of the Royal Society B*, **276**, 2015–2020.

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E. & Wilmers, C.C. (2009) Human predators outpace other agents of trait change in the wild. *Proceedings of the National Academy of Sciences of the United States of*

America, **106**, 952–954.

Diaz Pauli, B., Wiech, M., Heino, M. & Utne-Palm, A.C. (2015) Opposite selection on behavioural types by active and passive fishing gears in a simulated guppy Poecilia reticulata fishery. *Journal of Fish Biology*, **86**, 1030–1045.

Dochtermann, N.A., Schwab, T. & Sih, A. (2015) The contribution of additive genetic variation to personality variation: heritability of personality. *Proceedings of the Royal Society B*, **282**, 20142201.

Duffy, T.A., Picha, M.E., Borski, R.J. & Conover, D.O. (2013) Circulating levels of plasma IGF-I during recovery from size-selective harvesting in *Menidia menidia*. *Comparative Biochemistry and Physiology. Part A*, **166**, 222–227.

Fenberg, P.B. & Roy, K. (2008) Ecological and evolutionary consequences of size-selective harvesting: how much do we know? *Molecular Ecology*, **17**, 209–220.

Härkönen, L., Hyvärinen, P., Niemelä, P.T. & Vainikka, A. (2016) Behavioural variation in Eurasian perch populations with respect to relative catchability. *Acta Ethologica*, **19**, 21–31.

Härkönen, L., Hyvärinen, P., Paappanen, J., Vainikka, A. & Tierney, K. (2014) Explorative behavior increases vulnerability to angling in hatchery-reared brown trout (Salmo trutta). *Canadian Journal of Fisheries and Aquatic Sciences*, **71**, 1900–1909.

Heino, M., Díaz Pauli, B. & Dieckmann, U. (2015) Fisheries-induced evolution. *Annual Review of Ecology, Evolution, and Systematics*, **46**, 461–480.

Heino, M. & Godø, O.R. (2002) Fisheries induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science*, **70**, 639–656.

Hendry, A.P., Farrugia, T.J. & Kinnison, M.T. (2008) Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, **17**, 20–29.

Jakobsdottir, K.B., Pardoe, H., Magnusson, A., Björnsson, H., Pampoulie, C., Ruzzante, D.E. & Marteinsdottir, G. (2011) Historical changes in genotypic frequencies at the Pantophysin locus in Atlantic cod (*Gadus morhua*) in Icelandic waters : evidence of fisheries-induced selection ? *Evolutionary Applications*, **4**, 562–573.

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A., Johnston, F., Matsumura, S., Pardoe, H., Raab, K., Silva, A., Vainikka, A., Dieckmann, U., Heino, M. & Rijnsdorp, A.D. (2007) Managing evolving fish stocks. *Science*, **318**, 1247–1248.

Jørgensen, C. & Holt, R.E. (2013) Natural mortality: Its ecology, how it shapes fish life histories, and why it may be increased by fishing. *Journal of Sea Research*, **75**, 8–18.

Killen, S.S., Nati, J.J.H. & Suski, C.D. (2015) Vulnerability of individual fish to capture by trawling is influenced by capacity for anaerobic metabolism. *Proceedings of the Royal Society B*, **282**, 20150603.

Klefoth, T., Pieterek, T. & Arlinghaus, R. (2013) Impacts of domestication on angling vulnerability of common carp, Cyprinus carpio : the role of learning, foraging behaviour and food preferences. *Fisheries Management and Ecology*, **20**, 174–186.

Laugen, A.T., Engelhard, G.H., Whitlock, R., Arlinghaus, R., Dankel, D.J., Dunlop, E.S., Eikeset, A.M., Enberg, K., Jørgensen, C., Matsumura, S., Nusslé, S., Urbach, D., Baulier, L., Boukal, D.S., Ernande, B., Johnston, F.D., Mollet, F., Pardoe, H., Therkildsen, N.O., Uusi-Heikkilä, S., Vainikka, A., Heino, M., Rijnsdorp, A.D. &

Dieckmann, U. (2014) Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. *Fish and Fisheries*, **15**, 65–96.

Lone, K., Loe, L.E., Meisingset, E.L., Stamnes, I. & Mysterud, A. (2015) An adaptive behavioural response to hunting: surviving male red deer shift habitat at the onset of the hunting season. *Animal Behaviour*, **102**, 127–138.

Madden, J.R. & Whiteside, M.A. (2014) Selection on behavioural traits during 'unselective' harvesting means that shy pheasants better survive a hunting season. *Animal Behaviour*, **87**, 129–135.

Merilä, J. & Hendry, A.P. (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evolutionary Applications*, **7**, 1–14.

Milner, J.M., Nilsen, E.B. & Andreassen, H.P. (2007) Demographic side effects of selective hunting in ungulates and carnivores. *Conservation Biology*, **21**, 36–47.

Nannini, M.A., Wahl, D.H., Philipp, D.P. & Cooke, S.J. (2011) The influence of selection for vulnerability to angling on foraging ecology in largemouth bass Micropterus salmoides. *Journal of Fish Biology*, **79**, 1017–1028.

Olsen, E.M., Heupel, M.R., Simpfendorfer, C.A. & Moland, E. (2012) Harvest selection on Atlantic cod behavioral traits: implications for spatial management. *Ecology and Evolution*, **2**, 1549–1562.

Olsen, E.M. & Moland, E. (2011) Fitness landscape of Atlantic cod shaped by harvest selection and natural selection. *Evolutionary Ecology*, **25**, 695–710.

Ordiz, A., Støen, O.-G., Sæbø, S., Kindberg, J., Delibes, M. & Swenson, J.E. (2012) Do bears know they are being hunted? *Biological Conservation*, **152**, 21–28.

Palumbi, S.R. (2001) Humans as the World's grestest evolutionary force. *Science*, **293**, 1786–1790.

Philipp, D.P., Cooke, S.J., Claussen, J.E., Koppelman, J.B., Suski, C.D. & Burkett, D.P. (2009) Selection for vulnerability to angling in largemouth bass. *Transactions of the American Fisheries Society*, **138**, 189–199.

Pianka, E.R. (1970) On r- and K-Selection. *The American naturalist*, **104**, 592–597.

Pigeon, G., Festa-Bianchet, M., Coltman, D.W. & Pelletier, F. (2016) Intense selective hunting leads to artificial evolution in horn size. *Evolutionary Applications*, **9**, 521–530.

Postma, E. (2014) Four decades of estimating heritabilities in wild vertebrate populations: improved methods, more data, better estimates? in *Quantitative genetics in the wild* (eds A. Charmantier, D. Garant & L.E.B. Kruuk), Oxford University Press.

Price, E.O. (1984) Behavioral aspects of animal domestication. *The Quarterly Review of Biology*, **59**, 1–32.

Quinn, T.P., Hodgson, S., Flynn, L., Hilborn, R. & Rogers, D.E. (2007) Directional selection by fisheries and the timing of sockeye salmon (*Oncorhynchus nerka*) migrations. *Ecological Applications*, **17**, 731–739.

Raat, A.J.P. (1985) Analysis of angling vulnerability of common carp, *Cyprinus carp* L., in catch-and-release angling in ponds. *Aquaculture Research*, **16**, 171–187.

Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.-O. (2010) Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical transactions of the Royal Society B*, **365**, 4051–

4063.

Salinas, S., Perez, K.O., Duffy, T.A., Sabatino, S.J., Hice, L.A., Munch, S.B. & Conover, D.O. (2012) The response of correlated traits following cessation of fishery-induced selection. *Evolutionary Applications*, **5**, 657–663.

Sasaki, K., Fox, S.F. & Duvall, D. (2009) Rapid evolution in the wild: changes in body size, life-history traits, and behavior in hunted populations of the Japanese mamushi snake. *Conservation Biology*, **23**, 93–102.

Sutter, D.A.H., Suski, C.D., Philipp, D.P., Klefoth, T., Wahl, D.H., Kersten, P., Cooke, S.J. & Arlinghaus, R. (2012) Recreational fishing selectively captures individuals with the highest fitness potential. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 20960–20965.

Uusi-Heikkilä, S., Whiteley, A.R., Kuparinen, A., Matsumura, S., Venturelli, P.A., Wolter, C., Slate, J., Primmer, C.R., Meinelt, T., Killen, S.S., Bierbach, D., Polverino, G., Ludwig, A. & Arlinghaus, R. (2015) The evolutionary legacy of size-selective harvesting extends from genes to populations. *Evolutionary Applications*, **8**, 597–620.

Uusi-Heikkilä, S., Wolter, C., Klefoth, T. & Arlinghaus, R. (2008) A behavioral perspective on fishing-induced evolution. *Trends in Ecology & Evolution*, **23**, 419–421.

Vainikka, A., Tammela, I. & Hyvärinen, P. (2016) Does boldness explain vulnerability to angling in Eurasian perch Perca fluviatilis ? *Current Zoology*, **62**, 109–115.

Walsh, M.R., Munch, S.B., Chiba, S. & Conover, D.O. (2006) Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology*

Letters, **9**, 142–148.

Wilson, A.D.M., Binder, T.R., McGrath, K.P., Cooke, S.J. & Godin, J.-G.J. (2011) Capture technique and fish personality: angling targets timid bluegill sunfish, Lepomis macrochirus. *Canadian Journal of Fisheries and Aquatic Sciences*, **68**, 749–757.

Wilson, A.D.M., Brownscombe, J.W., Sullivan, B., Jain-Schlaepfer, S. & Cooke, S.J. (2015) Does angling technique selectively target fishes based on their behavioural type? *Plos One*, **10**, e0135848.