### Animal Behaviour 87 (2014) 129-135

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

### Selection on behavioural traits during 'unselective' harvesting means that shy pheasants better survive a hunting season

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### ARTICLE INFO

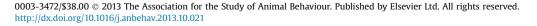
Article history: Received 17 April 2013 Initial acceptance 18 June 2013 Final acceptance 30 September 2013 Available online 21 November 2013 MS. number: 13-00336R

Keywords: boldness harvesting hunting personality Phasianus colchicus pheasant Recreational hunting can disrupt the population structure or alter the morphology of target populations. More subtly, such hunting may alter the behaviour of individuals in the target population, especially if individuals are culled nonrandomly. We assayed the behavioural temperaments of a sample of hand-reared and released pheasants, *Phasianus colchicus*. We could place birds on a behavioural continuum between bold or fast and shy or slow. Individual differences could not be explained by sex or mass. Birds were released into the wild and we followed their fate over a single hunting season. Birds that survived the hunting season were shyer or slower as juveniles than the original population mean. Males that died of disease or predation were relatively bold or fast as juveniles, while females dying of disease or predation were relatively bold or fast as juveniles were shot early in the season compared to females. Unselective hunting can skew the expression of behaviours in released gamebirds. This skew may explain why released birds subsequently fail to reproduce or are especially likely to die of natural causes once the hunting season has finished, and hence why it is difficult to establish wild populations of these species through reintroduction to an area where shooting takes place.

Hunting and harvesting impose selection pressures on the target population and lead to rapid evolutionary change in population structure, morphology and life history (Allendorf, England, Luikart, Ritchie, & Ryman, 2008; Allendorf & Hard, 2009; Darimont et al., 2009). In many cases, the strength of this effect is due to intentionally selective hunting or harvesting that targets individuals of specific age, size or sex (Fenberg & Roy, 2008; Milner, Nilsen, & Andreassen, 2007). However, in some systems such selectivity either cannot be practised because individuals in the population are similar or is not practised because of the hunting or harvesting method. Even without intentional selectivity in harvesting, removal of individuals from the population can be nonrandom, with particular age, sex or growth rate classes being overrepresented (Biro & Post, 2008; Bunnefeld, Baines, Newborn, & Milner-Gulland, 2009), and this can lead to disturbance of population dynamics (Bunnefeld, Reuman, Baines, & Milner-Gulland, 2011).

A less studied effect of hunting and harvesting is the change in behaviour of individuals in a target population. Individuals living in hunting areas are typically more vigilant and show greater flight distances than conspecifics in areas without hunting (Donadio & Buskirk, 2006; Setsaas, Homern, Mwakalebe, Stokke, & Røskaft, 2007). Behavioural changes resulting from hunting may be plastic, with individuals becoming more vigilant or moving to denser cover when the hunting season starts (Brøseth & Pedersen, 2010; Kilgo, Labisky, & Fritzen, 1998). However, a long-term study suggests that these changes may be inherited, with selection through hunting acting to increase flight distance across years as hunting pressure increases (Reimers, Loe, Eftestøl, Colman, & Dahle, 2009).

Hunting and harvesting may impose cryptic selection pressures on complex behavioural assemblages. These behavioural temperaments, also described as syndromes, coping styles, types or personalities (Réale, Reader, Sol, McDougall, & Dingemanse, 2007), capture a suite of correlated behaviours that are consistent across time and contexts. The rigidity of these behavioural consistencies allows assays to be conducted at one time that are meaningful at a later stage (Bell, Hankison, & Laskowski, 2009; but see Dingemanse, Kazem, Réale, & Wright, 2010). These behaviours are heritable, and subject to natural selection (Dingemanse & Réale, 2005). Typically, individuals can be ordered along a series of temperament axes. A commonly used axis orders individuals by how bold or shy they are (Smith & Blumstein, 2008). Position along the temperament continuum confers differing fitness payoffs (Smith & Blumstein, 2008) and although this trade-off may vary with ecological conditions and population composition, it can also maintain variation in temperament within a population (Dall, Houston, & McNamara, 2004). In artificial harvesting experiments, bold, active and fastgrowing fish were disproportionately caught in nets, providing an



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explanation for why in harvested populations of fish, slow growth rates, and perhaps less bold or active behaviours, have repeatedly evolved (Alós, Palmer, & Arlinghaus, 2012; Biro & Post, 2008). In a real-world hunting scenario, elk, *Cervus elaphus*, that were killed by hunters had moved faster and were described as behaving more boldly prior to death than those that were not shot (Ciuti et al., 2012). Therefore, we may expect that selection imposed by shooting may have effects on behaviours other than those directly selected by shooting.

Hunting of pheasants, Phasianus colchicus, using the method of driven shooting in the U.K. is generally considered to be a nonselective process, with birds of all ages and either sex being shot as they fly, having been flushed from cover by dogs or humans (Hill & Robertson, 1988a). Despite the assumption of nonselectivity, there has previously been concern that unintentional selection is effected during driven shooting. In the sexually monomorphic red grouse, Lagopus lagopus, which is also subjected to driven shooting, disproportionately more young birds and old males are shot when bag sizes are large (Bunnefeld et al., 2009). In pheasants, there have been concerns over the effects of shooting not on sex or age of the birds, which appear to be shot in proportion to numbers driven up (Hill & Robertson, 1988a), but on heritable traits, specifically those of interest to hunters, namely flying ability and body size (Robertson, Wise, & Blake, 1993). Despite these concerns, there appeared to be no effect of shooting selectivity on these traits (Robertson et al., 1993). One explanation for this is that the population of pheasants being shot is supplemented each year by large numbers of birds reared in captivity and released into the wild. However, although captive breeding may maintain behavioural variation in the extremely large population of released pheasants, any selection on behavioural traits could lead to skew in the behaviour of the much smaller wild population with which the large numbers of survivors of a shooting season may interbreed.

In this study we asked whether pheasants were being culled selectively according to their behavioural temperament, despite no efforts by the hunters to target this attribute. We controlled for an individual's morphology and sex as both of these may help explain differences in movement, conspicuousness or other influences on survival (Turner, 2007). We assayed the temperaments of a large number of young pheasants prior to release, and followed their fates through the subsequent hunting season and beyond. We then specifically tested whether those surviving the season were a representative sample of the range of behavioural temperaments released at the start of the season, whether the cause of death varied with behavioural temperament, and whether the time in the season when a bird was shot was related to an individual's temperament.

### METHODS

### Rearing, Releasing and Recovering Birds

Chicks were reared on a commercial game farm from 1 day old in spring 2011. Day-old chicks were reared in groups each of about 120. They were placed in a 1 m diameter plywood circle inside a shed where they were warmed using gas heaters and given access to food and water (commercial, age-appropriate feeder pellets provided ad libitum in standard plastic feeders, and water supplied ad libitum through standard plastic drinkers). After 1 week, the plywood circle was removed and the chicks had access to the  $1.3 \times 1.3$  m shed, and after a further week they were given daily access to a 'shelter pen' measuring  $2.4 \times 2.4$  m with enclosed side walls, a roof of clear plastic and a gravel floor. When the chicks were 3 weeks old, the gas heaters were turned off and the birds were given free access to outdoor, grass-floored, open pens measuring  $3.5 \times 20$  m where additional ad libitum food and water were provided. Pens were in visual but not auditory isolation from other pens. When the birds were 4 weeks old, we took 450 at random from the population, exposed each to a series of three consecutive behavioural tests (see below) and weighed them.

At 7 weeks, all poults were sexed visually and taken to a release site. The poults were placed in a large (ca.  $70 \times 60$  m) open-topped pen on a shooting estate in woodland in mid-Devon, U.K. Here, they were surrounded by fencing about 2 m high and electric wires to exclude foxes. The pen contained feeders and drinkers that provided ad libitum access to food and water (mixed wheat and commercial age-appropriate feed pellets supplied via hopper feeders with water supplied via nipple drinkers). The pen contained a large quantity of natural cover in the form of trees and shrubs, as well as five artificial shelters offering protection from the weather. Birds could disperse from the pen at will by flying over the fence, and could re-enter it easily using one-way gateways designed to exclude foxes. Birds were encouraged to leave the pen and disperse into the surrounding area by provision of feed hoppers placed in woodland, hedgerow and cover crops. The location of the centre of the pen was measured using GPS (Garmin eTrex).

Birds were recovered in three different ways over the following year. First, birds that had died of natural causes were collected by searching. Prior to the hunting season, the pen and surrounding area was visited at least twice a week by us and a gamekeeper with dogs. After the shooting season, the same area was visited less frequently, typically once per 2-3 weeks. We picked up any carcasses of pheasants that we found and identified them by their numbered wing tag. Some dead birds were damaged, indicating that they had been predated. If there was no external damage to the bird, we suspect that it died of other causes, perhaps disease. However, it is possible that birds we recovered with marks of predation had actually died of other causes and their body had been scavenged. Therefore, we could not confidently discriminate natural causes of death and so we combined them into a single category. Prior to the start of the hunting season, we recovered 22 males and 15 females that were tagged and had died of natural causes. Following the hunting season, we recovered seven dead birds, including two that had also been seen after the first hunting season (see below). We recorded the location of where birds were recovered either using GPS or for birds that were returned to us, by plotting the recovery location on a 1:25 000 Ordnance Survey map in consultation with the person recovering the bird. Second, birds were shot as part of a number of commercial pheasant shoots. Shooting took place once every 2 weeks on the central study site and on other dates on neighbouring land between October 2011 and February 2012. We recovered 70 males and 46 females that were tagged and had been shot. Neighbouring shoots occasionally only returned the tags and kept the bird, or delayed return of the bird such that taking accurate morphological measures was not possible. Shooting typically took the form of a 'driven' shoot in which 6–10 guns (hunters armed with shotguns) were positioned in a line and a team of beaters and their dogs then walked towards them, flushing birds from the undergrowth in front of them so that they flew towards the line of guns and were shot at. The guns were unaware of the hypotheses being investigated and shot at birds as they presented themselves. We recorded the location of the drive from which birds had been shot as it was not safely possible to mark accurately where they flew from during the middle of shooting, with each drive centre being measured using GPS. We measured the distance dispersed as the linear distance between the release point and the drive or location from where they were recovered. Because birds and tags were returned to us by neighbouring shoots on a somewhat ad hoc basis, we could not accurately determine the dates the birds were shot. Therefore, we divided the season in half

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