



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



Joah R. Madden*, Mark A. Whiteside

Centre for Research in Animal Behaviour, Psychology, University of Exeter, Exeter, U.K.

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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 shy or slow. Males that were 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.

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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 fast-growing fish were disproportionately caught in nets, providing an

* Correspondence: J. R. Madden, Centre for Research in Animal Behaviour, Psychology, University of Exeter, Exeter EX4 4QG, U.K.

E-mail address: J.R.Madden@exeter.ac.uk (J. R. Madden).

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 (Bunnfeld 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 × 1.3 m shed, and after a further week they were given daily access to a 'shelter pen' measuring 2.4 × 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 × 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 × 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

and we could confidently assign birds as having been shot in the early or late part of the season. Finally, we visited the field site after the shooting season between February and May 2012 as part of another study and the gamekeeper also visited it at least twice weekly for his work. During this time we recorded the tag numbers of birds that we observed alive there (three males and seven females); birds that we recovered on the site that we knew from the freshness of their bodies had died after the shooting season (four males and one female) and a single bird (male) shot in the subsequent hunting season to give us a sample of 16 birds that had survived the initial hunting season.

For birds that were shot, we measured them as soon after shooting as was possible and safe. We recorded the location where they had been shot. Mass was measured using a Salter Super Samson spring balance (precision = 10 g). Tail length was measured using a steel rule under the longest central tail feather and excluding birds that had lost such feathers (precision 1 mm). Mean wing length was calculated from measures of the left and right wing chords using a stopped wing rule (precision 1 mm). Mean tarsus length was calculated from measures of the left and right tarsi using callipers (precision = 0.1 mm). Mean wattle area was calculated from measures of the maximum height and orthogonal width of the left and right wattles, measured using callipers.

Behavioural Testing of Birds

Response to a novel environment

A bird was caught from its rearing pen using a hand net and immediately placed into a plastic crate measuring 0.95 × 0.65 m and 0.27 m high. The crate floor was covered with a green Styrofoam board marked out in 20 cm squares and the crate walls were covered with the Styrofoam sheets ensuring that the bird was in visual but not auditory isolation from others. The bird was placed into the central square and left for 1 min. We measured the individual's response to this novel environment by determining its activity level, directly observing the bird from above while positioned behind a screen, and counting the squares entered during a 1 min focal follow. A new square was entered when the outside toe of the right foot was placed in a square separate from its previous position. The same square that was left and subsequently re-entered was counted twice.

Response to a novel object

Immediately after Test 1 (Response to a novel environment) was completed, we placed a novel object (a blue beaker measuring 8 cm diameter × 17 cm tall) three squares away from the bird. The beaker was selected because it was of a colour and shape not encountered in the rearing environment. We then timed how long the bird took to touch the beaker with any part of its body (precision = 1 s). If birds took longer than 3 min, we recorded a time of 180 s and ended the test.

Response to novel social stimuli

Immediately after Test 2 (Response to a novel object) was completed, we removed half of one of the sheets on the wall of the crate to expose a neighbouring crate in which we placed five other mixed-sex, 4-week-old pheasants that were unknown to the test bird. We moved the test bird to the square furthest from the exposed crate and then timed how long it took the test bird to place the outside toe of its right foot into the square closest to the crate. If birds took longer than 3 min, we recorded a time of 180 s and ended the test.

After being tested, each chick was weighed and individually marked using a numbered plastic wing tag (Roxan Ltd, Selkirk,

U.K.). A random sample of 21 birds (limited by the remaining daylight hours on the day of testing) was recaptured 4 h after initial testing and retested following the same methods. We used these assays to determine how repeatable our measures were following methods described in Lessells & Boag (1987).

Ethical Note

All birds were reared as part of a larger breeding programme by a commercial game breeder using procedures that met or exceeded the DEFRA Code of Practice for the Welfare of Gamebirds Reared for Sporting Purposes (https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/69379/pb13356-game-birds-100720.pdf). All birds were visited daily by the game breeder. For all behavioural testing of birds individuals were in visual but not auditory isolation from flockmates for up to 5 min, and then in visual contact with flockmates, but unable to touch them directly for up to a further 3 min. All birds, apart from the 21 repeat measures, were tested only once each. Released birds were attended by the gamekeeper who ensured they had ad libitum food and water supplies as well as administering appropriate drugs if he detected disease among birds in the release pens. Once birds had dispersed beyond the release pens, the gamekeeper maintained food and water supplies via hopper feeders. The birds were shot as part of a commercial hunting operation and were not specifically shot for this study. We made use of data from birds recovered from the hunting area. All measurements used in this study were collected from birds that were dead. The work was approved by the University of Exeter Psychology Ethics Committee (Approval 2007/015).

Statistical Analysis

We used principal component analysis (PCA) to collapse the three behavioural assays into a single measure. We extracted components with eigenvalues > 1. We generated PC scores based on all 450 birds in addition to the 21 repeated measures that we collected. This enabled us to consider the repeatability of the extracted PCA scores that we used in subsequent analyses. The PCA gave us a population mean score of 0, against which we could compare scores of recovered birds.

We asked whether an individual's PCA score was simply related to any of its morphological measures (tail, wing or tarsus length, mass or wattle area) using a Pearson correlation. We conducted these correlations separately for each sex, given the marked sexual dimorphism in the species.

We used a general linear model (GLM) to explore individual differences in PCA scores, including an individual's sex and its mass at testing when 4 weeks old as possible explanatory variables, and the interaction between these two main effects. This analysis included 450 birds. We used a second GLM to test whether birds that were shot differed in their PCA scores from those that died natural deaths, while accounting for their sex. This analysis included 153 birds. We used a third GLM to test whether an individual's PCA score predicted when in the season it was shot, while controlling for a bird's sex. We assigned shot birds to one of two categorical classifications: early (October/November) or late (December/January) season. This analysis included 115 birds. We used a fourth GLM to ask whether an individual's dispersal distance was predicted by their PCA score, while controlling for an individual's sex and its age at shooting. This analysis included 164 birds. For all models, the normality of residuals was confirmed. We used one-sample *t* tests to compare the juvenile temperament of both birds that died and the 16 birds that survived the hunting

season to the temperament population mean. All analyses were conducted using SPSS v19.

RESULTS

We extracted a single principal component score from the three behavioural measures that we collected. This explained 57% of the variance in the measures and had positive loadings for time taken to touch a novel object (0.89) and time taken to approach conspecifics (0.34), and a negative loading for level of activity in the novel environment (-0.90). Therefore, an individual with a positive PCA score tended to take a long time to approach a novel object or novel conspecifics, and was not very active in the novel environment. Such an individual could be described as shy or slow (hereafter, shy). Conversely, an individual with a negative PCA score tended to approach novel objects and novel conspecifics rapidly, and was active when in a novel environment. Such an individual could be described as bold or fast (hereafter, bold). Intraindividual repeatability of PCA scores was fairly high ($r = 0.70$, $F_{20,42} = 2.37$, $P = 0.028$).

Pheasant PCA scores did not differ by sex or according to an individual's mass at testing (GLM: sex: $F_{1,450} = 0.19$, $P = 0.66$; mass: $F_{1,450} = 0.03$, $P = 0.86$; sex*mass: $F_{1,450} = 0.04$, $P = 0.85$). We found no correlations between five measures of an adult's morphology and its PCA score derived as a juvenile for either males or females, even before correcting for multiple comparisons (Table 1).

Males dying of natural causes including disease and predation were bold as juveniles, with scores at the negative end of the PCA continuum, compared to males that were shot, while females dying of natural causes were shy as juveniles with positive scores compared to females that were shot (GLM: sex*cause of death: $F_{1,153} = 4.50$, $P = 0.036$; Fig. 1). Regardless of cause of death, females that we recovered had higher PCA scores as juveniles and were shyer than males (sex: $F_{1,153} = 10.43$, $P = 0.002$). Across the sexes, juvenile PCA scores of birds dying a natural death did not differ from those of birds that were shot (cause of death: $F_{1,153} = 0.16$, $P = 0.69$). Compared to the original population, females that died of natural causes were shy, with higher juvenile PCA scores than the original population mean (one-sample t test: $t_{15} = 5.38$, $P < 0.001$). Males that were shot or died of natural causes and females that were shot did not differ from the original population mean (one-sample t tests: all $P > 0.16$).

Males classed as bold when juvenile were shot first. Males shot early in the season had lower juvenile PCA scores than males that

Table 1
Pearson correlations between an individual's PCA score and five morphological measures

Morphological measure		Males	Females
Tail (mm)	r	0.12	0.13
	P	0.38	0.39
	N	55	45
Mass (g)	r	0.23	-0.01
	P	0.08	0.94
	N	62	45
Mean wing length (mm)	r	0.15	0.15
	P	0.23	0.32
	N	62	45
Mean tarsus length (mm)	r	-0.01	-0.01
	P	0.92	0.97
	N	62	45
Mean wattle area (mm ²)	r	0.04	-0.04
	P	0.78	0.80
	N	61	45

Variation in sample sizes is due to damage to some birds preventing accurate measurement.

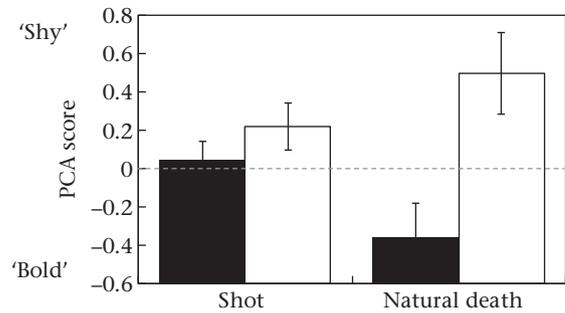


Figure 1. Mean juvenile PCA scores for male (black bars, $N = 92$) and female (white bars, $N = 61$) pheasants recovered from the wild, at least 4 weeks after release, either through shooting or by recoveries of bodies and so considered to have died a natural death through disease or predation. Error bars indicate ± 1 SE. The dashed line indicates the original population mean PCA score.

shot late in the season, whereas females shot early in the season had similar juvenile PCA scores to those shot later in the season (GLM: sex*stage of season: $F_{1,115} = 6.17$, $P = 0.014$; Fig. 2). Overall, mean juvenile PCA scores of shot birds did not change as the season progressed (stage of season: $F_{1,115} = 2.78$, $P = 0.10$) and the sexes did not differ in their mean PCA scores (sex: $F_{1,115} = 1.04$, $P = 0.31$). Females shot early in the season and males shot later in the season were shy as juveniles, having higher PCA scores than the original population mean (early females: $t_{20} = 2.27$, $P = 0.034$; late males: $t_{29} = 4.17$, $P < 0.001$).

The distance that recovered birds dispersed from the release pen was not related to their juvenile PCA score (Table 2). Birds classed as bold when juveniles did not disperse further as adults. Instead, dispersal distance increased as the season progressed, with all birds regardless of sex or PCA score being found further from their release points (Table 2).

The 16 recovered or resighted birds that survived the hunting season were shy as juveniles with higher PCA scores (mean \pm SD = 0.43 ± 0.39) than the original population mean (one-sample t test: $t_{15} = 4.40$, $P = 0.001$). All these individuals apart from one (a female found dead) had PCA scores greater than the original population mean.

DISCUSSION

Pheasants that survived the shooting season were predominantly shyer as juveniles than the mean of the population that were released at the site. It is perhaps surprising that a behavioural assay conducted early in life should provide a good predictor of an

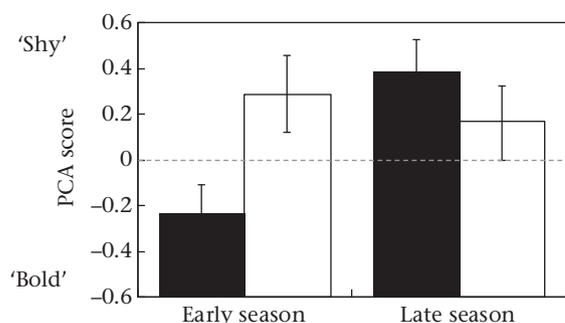


Figure 2. Mean juvenile PCA scores for male (black bars, $N = 69$) and female (white bars, $N = 46$) pheasants shot during the shooting season, either early (October/November) or late (December/January). Error bars indicate ± 1 SE. The dashed line indicates the original population mean PCA score.

Table 2
Terms predicting variation in dispersal distance for released pheasants

Terms	df	$F_{df,164}$	P
Sex	1	2.05	0.16
PCA score	1	0.07	0.79
Date	7	6.17	<0.001
Date*PCA score	7	0.92	0.50
Sex*Date	6	0.89	0.51
Sex*PCA score	1	2.19	0.14
Sex*Date*PCA score	6	0.57	0.75

$N\delta = 88$, $\text{♀} = 76$.

individual's fate several months later. Whether an individual's temperament or personality remains consistent throughout life remains unresolved (e.g. Dingemanse et al., 2010; Réale, Gallant, Leblanc, & Festa-Bianchet, 2000). We cannot be certain that the behavioural traits that we measured at 4 weeks old are homologous to those that determine adult fate, but we suspect that they correlate with adult behaviours pertinent to their survival. This may explain why our results mirror those seen in elk and fish populations in which slow or shyer individuals appear to be more likely to survive hunting or harvesting pressures (Alós et al., 2012; Biro & Post, 2008; Ciuti et al., 2012). The disproportionate survival of shy pheasants could be for one of four reasons. First, birds classed as bold when juveniles may have dispersed further and left the study site, and were thus unavailable for recapture or resighting, leading to a bias in the birds that we detected at the end of the shooting season. Such relationships are seen in some species of fish, lizards and birds (Cote & Clobert, 2007; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010; Dingemanse, Both, van Noordwijk, Rutten, & Drent, 2003). This is unlikely to explain the pattern in our data, however, given that we found no relationship between an individual's juvenile PCA score and the distance it had dispersed prior to being shot. We also received no reports of recaptures or resighting of our tagged birds on the neighbouring shoots once the hunting season had ended. The land that these neighbouring shoots covered extends for up to 4 km from the central release points which is about four times the mean dispersal distance recorded from radiocollared pheasants ($\delta = 783$ m, $\text{♀} = 1053$ m) and almost that of the maximum distance that any radiocollared bird moved (4685 m; Turner, 2007). Therefore, we believe that we were unlikely to miss recording a substantial number of birds that dispersed a long distance. Second, an individual's juvenile PCA score may have been related to its morphology (as reported by Colléter & Brown, 2011), such that any differences in survival that we detected were simply driven by differences in body or trait size that were preferentially targeted by the guns. We think this unlikely given that we found no relationships between any of five adult morphological measures and an individual's juvenile PCA score. Third, shy birds may have been unusually susceptible to resighting or recapture in large walk-in traps deployed by the gamekeeper. In terms of resighting, we searched the site at the end of the hunting season, with dogs and humans, to flush out birds in a similar manner to that practised during the shooting season, and so we suspect that our sampling methods did not induce bias. We cannot be certain that our resampling method was not biased towards shy birds (see Carter, Goldizen, & Tromp, 2010; Wilson, Binder, McGrath, Cooke, & Godin, 2011), but given the result of our behavioural assays that showed shy birds took longer to approach novel objects, we would be surprised if these same birds when adults were disproportionately attracted towards observers or novel trapping apparatus. The final explanation, which we believe to be most likely, is that birds classed as bold when juveniles may have died disproportionately before and during the shooting season.

Males classed as bold when juveniles were disproportionately likely to die of natural causes, typically before the breeding season. These natural causes included both predation and disease. Pheasants are frequently killed by both avian and ground predators (Hill & Robertson, 1988a). In fish, lizards and swift foxes, *Vulpes velox*, bolder individuals appear to be more susceptible to predation (Dugatkin, 1992) or predation attempts (Carter et al., 2010), or unspecified causes of mortality (Bremner-Harrison, Prodohl, & Elwood, 2004). This may be because they are more active and so more likely to be exposed to predators, or, being more willing to investigate novel stimuli or locations, they spend longer in less preferred and potentially more dangerous habitats. Similar explanations may apply to our adult pheasants. About 10% of released pheasants die of disease (Turner, 2007). An individual's response to disease and stress can be related to its behavioural temperament (Cavigelli, 2005). In birds, shy individuals tend to respond to stress with strong HPA (hypothalamic–pituitary–adrenal) activity and a resulting increase in circulating glucocorticoids (Carere, Caramaschi, & Fawcett, 2010). Therefore, shy birds may be more susceptible to disease, if not to predation. This may partially explain why females classed as shy or slow when juveniles were disproportionately likely to die of natural causes. However, it is difficult to explain why bold males but shy females were more likely to die of natural causes. It could be that males were more likely to be predated, while females were more likely to die of disease. We suspect that the larger, noncryptic male pheasants were more susceptible to predation than females, as is the case in many sexually dimorphic species (Andersson, 1994). Unfortunately, we cannot reliably ascribe cause of death to the birds that we recovered. Carcasses bearing obvious signs of having been eaten by predators could have died of disease prior to being eaten, or sublethal effects of stress or disease may have increased the likelihood of predation.

Males shot early in the season were disproportionately bolder as juveniles than those shot later in the season. This suggests that driven pheasant shooting is not as unselective as is believed, but that there is a bias, at least in the male pheasants being shot. Obviously, the hunters shooting the pheasants had no knowledge or cues as to the behavioural scores that pheasants had, so we do not believe that the bias is intentionally driven by the behaviour of the hunters. Instead, we believe that the bias is due to differences in the flight behaviour of the male pheasants. We suspect that bold or fast males in general may react to threats in their environment with a 'fight-or-flight' response, and in these specific circumstances may more readily take flight when disturbed by the beaters than shy or slow individuals which may typically show a 'freeze-hide' response (Korte, Koolhaas, Wingfield, & McEwen, 2005). This results in bold males flying higher over the hunters, having taken off earlier and so had an opportunity to gain height and be the first birds to fly over the line of hunters. Both these behaviours make them more likely to be shot. Hunters are more likely to shoot at high birds (Robertson, 1997). We noted that the hunters on this shoot, in common with those on most other U.K. shoots, refrained from shooting birds that were running on the ground or flying low to the ground. This restraint is due to both safety considerations (shooting at low birds increases the likelihood of hitting neighbouring hunters with direct fire) and sporting considerations (low-flying birds are not considered challenging shots and hunters shooting low birds were shouted at and ridiculed by other hunters). The flight behaviour of pheasants is not predicted by their strain or rearing condition, but is related to their mass, with lighter birds generally taking off at a steeper angle and flying higher (Robertson et al., 1993). Flight height is also related to the distance from take-off, with birds taking off earlier reaching greater heights over the hunters. Birds taking flight early in a drive face a second challenge. The first birds flying across a line of hunters are more likely to be shot than later birds

because having shot at the first bird, the hunter needs to reload the gun, which can mean that the later bird can pass over unscathed. As the shooting season progresses, the relative balance of bold and shy birds changes as bold males are removed from the population. This leaves shy males overrepresented and thus shot later on. Females did not show a similar pattern, with the juvenile PCA scores of shot birds remaining fairly consistent throughout the shooting season. This may be because, for females, juvenile PCA score does not predict flight distance from disturbance, with both shy and bold females relying on their cryptic plumage to conceal them from threat, resulting in females across the boldness spectrum taking flight in a similar way in response to disturbance.

An overrepresentation of shy individuals in the surviving population is likely to have consequences for the population structure in subsequent years in two ways. First, many commercial shoots collect up adults at the end of the hunting season to breed from for the next season. We do not have measures of the heritability of our measures of behavioural temperament, but, in other birds, heritability of such behavioural temperaments is about 20–40% (e.g. Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002). Therefore, these captured birds are likely to produce offspring with behavioural temperaments similar to themselves, meaning that the population released the following summer is, on average, shyer than the previous year. This means that the released birds may be more susceptible to natural death (disease or predation). They may also fly differently, which would affect the recreational aspects of pheasant shooting and consequently the economic balance of the activity. Such mechanisms may explain the change in flight distances seen in reindeer, *Rangifer tarandus*, as hunting levels increased in a population (Reimers et al., 2009). Similar concerns may be seen in the offspring of birds that are not captured but left to breed in the wild. However, the reproductive success of released pheasants in the year following release is extremely poor (Hill & Robertson, 1988b). This poor performance may be a direct result of an individual's behavioural temperament, and therefore a second mechanism by which the population skew has an impact. Bold and aggressive (but not more exploratory) individuals typically have higher reproductive success (Smith & Blumstein, 2008). This may be because they are more preferred as mates (Godin & Dugatkin, 1996), and consequently fewer of them provide less choice for females. Bold individuals may be relatively better able to defend mates or resources from other shyer individuals. If so, changes in mean population temperament are likely to have little effect, as shy individuals simply compete with other shy individuals. Alternatively, poor reproductive success may be because shy individuals are less efficient at performing behaviours such as parental care or foraging. Shy female eider ducks, *Somateria mollissima*, with long flight initiation distances incubated for shorter periods, resulting in offspring of lower quality (Seltmann et al., 2012). Male convict cichlids, *Cichlasoma nigrofasciatum*, that were less active in the presence of novel individuals provided less parental care (Budaev, Zworykin, & Mochek, 1999). Bold agamas, *Agama planiceps*, spent more time foraging (Carter et al., 2010) and shoals of bold guppies, *Poecilia reticulata*, were more efficient foragers (Dyer, Croft, Morrell, & Krause, 2009). Released pheasants are usually fed by gamekeepers with grain, but this supplementary feeding is usually withdrawn at the end of the hunting season, forcing surviving birds to switch rapidly to novel natural food supplies (Hoodless, Draycott, Ludiman, & Robertson, 1999). If shy birds are less likely to sample novel food supplies, they may starve or enter the breeding season in poor condition. Given that only 16% of released birds survive the shooting season to breed (Turner, 2007), and their reproductive output is so low compared to wild birds, the effect on the population might be assumed to be negligible. However, these weak individual effects are offset by the sheer numbers of birds released for

shooting in the U.K. Around 35 million pheasants are released each year across almost all of lowland rural U.K. (PACEC, 2006), swamping a naturalized breeding population of around 2.3 million birds (Gibbons, Reid, & Chapman, 1993). Therefore, even with a relatively low individual contribution to population fitness (not considering effects such as competition for resources or habitat) the overall effect on wild stocks is likely to be substantial. It would be instructive to explore whether individual juvenile temperament also predicts adult responses in contexts other than hunting, such as mating success, parental care or foraging decisions. In addition, it would be helpful to compare temperaments of birds drawn from the wild population with those of birds in captive breeding populations to determine whether this unintentional selection is leading to evolutionary change.

Driven shooting, as commonly practised in the U.K., leads to unintentional selective harvesting of pheasants according to an individual's behavioural temperament, with shy juveniles being most likely to survive from release to the start of the following breeding season. Similar effects of unintentional selective harvesting were seen in the population dynamics of red grouse, *Lagopus lagopus*, shot in a similar manner (Bunnefeld et al., 2011). The effects that we see on the distribution of behavioural temperaments may have more far-reaching consequences, mediating individual responses to human contact, hunting, habitat disruption and disease transmission (McDougall, Réale, Sol, & Reader, 2006). If juvenile temperament corresponds to adult temperament then this skew within the population, with an underrepresentation of bold or fast birds recruiting to the breeding population, may help explain why pheasants that survive the shooting season exhibit poor reproductive output in the wild. If temperament is heritable, then such unintentional selection is likely to lead to evolutionary changes (Allendorf & Hard, 2009), and given the free mixing of truly wild pheasant populations and captive-reared, released birds, we believe that pheasant hunting could influence the evolutionary trajectory of the wild stock in the U.K.

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