Diet complexity in early life affects survival in released pheasants by altering foraging efficiency, food choice, handling skills and gut morphology

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Summary

1. Behavioural and physiological deficiencies are major reasons why reintroduction programmes suffer from high mortality when captive animals are used. Mitigation of these deficiencies is essential for successful reintroduction programmes.

2. Our study manipulated early developmental diet to better replicate foraging behaviour in the wild. Over 2 years, we hand-reared 1800 pheasants (*Phasianus colchicus*), from 1 day old, for 7 weeks under different dietary conditions. In year one, 900 pheasants were divided into three groups and reared with (i) commercial chick crumb, (ii) crumb plus 1% live mealworm or (iii) crumb plus 5% mixed seed and fruit. In year two, a further 900 pheasants were divided into two groups and reared with (i) commercial chick crumb or (ii) crumb plus a combination of 1% mealworm and 5% mixed seed and fruit. In both years, the commercial chick crumb acted as a control treatment, whilst those with live prey and mixed seeds and fruits mimicking a more naturalistic diet. After 7 weeks reared on these diets, pheasants were released into the wild.

3. Postrelease survival was improved with exposure to more naturalistic diets prior to release. We identified four mechanisms to explain this. Pheasants reared with more naturalistic diets (i) foraged for less time and had a higher likelihood of performing vigilance behaviours, (ii) were quicker at handling live prey items, (iii) were less reliant on supplementary feed which could be withdrawn and (iv) developed different gut morphologies.

4. These mechanisms allowed the pheasants to (i) reduce the risk of predation by reducing exposure time whilst foraging and allowing more time to be vigilant; (ii) be better at handling and discriminating natural food items and not be solely reliant on supplementary feed; and (iii) have a better gut system to cope with the natural forage after the cessation of supplementary feeding in the spring.

5. Learning food discrimination, preference and handling skills by the provision of a more naturalistic diet is essential prior to the release of pheasants in a reintroduction programme. Subsequent diet, foraging behaviour, gut morphology and digestive capabilities all work together as one nutritional complex. Simple manipulations during early development can influence these characteristics to better prepare an individual for survival upon release.

Key-words: antipredator behaviour, conservation, diet, foraging, learning, *Phasianus colchicus*, pheasant, reintroduction, survival

Introduction

Captive-reared animals released as a result of reintroduction programmes suffer from extremely high mortality (Kleiman 1989; Snyder *et al.* 1996), significantly higher than their wild conspecifics (Fischer & Lindenmayer 2000). One cause may be due to the genetic differences between wild and captive-reared individuals, which can arise if a small founder population in captivity are highly inbred or genetically adapted to conditions different to those found at the site of release (Armstrong & Seddon 2008). However, although released animals commonly have low survival and reproductive success, their surviving

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wild offspring are often equally successful as their wild peers (Sage *et al.* 2003), suggesting that physical and behavioural characteristics influenced by early life experiences are at fault (Snyder *et al.* 1996; van Heezik & Seddon 1998). The effects of rearing conditions can be profound during the early stages of development (Desai & Hales 1997; Latham & Mason 2008) and can persist after independence (Cam, Monnat & Hines 2003), influencing adult survival and reproduction (Lindström 1999). When an individual is subjected to unnatural or artificial rearing conditions prior to release, they may lack opportunities to acquire essential survival skills such as predator detection and avoidance (Kleiman 1989; Griffin, Blumstein & Evans 2000), food acquisition and processing (Ellis *et al.* 2000), social behaviour (Fleming & Gross 1993) and locomotion (Hill & Robertson 1988). These behavioural deficiencies may be an important reason for the high mortality and poor success of reintroduction programmes (Kleiman 1989; Fischer & Lindenmayer 2000). The continued low success rates found in reintroduction programmes have prompted calls for a more concerted effort to understand the cause of behavioural deficiencies and to develop ways of mitigating their impact (Kleiman 1989; Seddon, Armstrong & Maloney 2007). However, the nature of reintroduction programmes, focussing on rare and endangered species, often makes more fundamental research difficult and can have poor monitoring (Armstrong & Seddon 2008), insufficient project duration (Beck *et al.* 1994) and a reluctance to report failure (Sarrazin & Barbault 1996). Furthermore, recovery programmes can lack the sample sizes to allow for controlled and replicable conditions required for detailed analysis (Armstrong & Seddon 2008). In order to investigate the effects of early rearing conditions, it is necessary to use a system in which large numbers of individuals can be reared under a range of controlled conditions and their survival accurately monitored postrelease.

Pheasants (*Phasianus colchicus*), reared and released in the United Kingdom for recreational shooting, offer an introduction programme that avoids such confounds and complications found with work on endangered species, with vast numbers of individuals being used each year offering a unique opportunity to investigate the role of early rearing on behavioural development and the consequent fate of introduced birds. Up to 35 million birds are released each year to supplement wild stock for shooting (PACEC 2008) and typically around 25% of released birds die in the 3- to 4-month period after release and before shooting begins (Turner 2004). Wild-born pheasants show better survival compared to those reared and released birds (Hill & Robertson 1988; Brittas *et al.* 1992; Leif 1994). Pheasants face three distinct threats postrelease. First, released pheasants are more vulnerable to predation than their wild conspecific (Hessler *et al.* 1970; Sage & Robertson 2000). Secondly, birds are unable to maintain body condition when released into the wild, which is often attributed to poor foraging efficiency after

release (Brittas *et al.* 1992; Sage & Robertson 2000). Thirdly, birds may develop a high dependence on supplementary feeding which is commonly withdrawn in the spring and are often unable to make the transition between the supplementary fed diets and more a natural diet (Draycott *et al.* 1998).

We concentrated on the diet that chicks experienced early in life and asked how simple supplementation of standard, homogenous commercial rearing feed may provoke complex and long-lasting behavioural and physiological developments that impact on the fate of the released birds. Pheasants are naturally omnivores, utilizing a wide range of food items (Hill & Robertson 1988). Pheasants typically follow their mother to sites to learn about food (Hill 1985). Captive rearing may inhibit individual opportunities for learning and exposure to different food types. This likely impacts on two mechanisms pertaining to diet which may influence individual chances of survival upon release: increased foraging efficiency and increased dietary breadth.

Developing an efficient foraging technique means that a bird can ingest more food, increasing their body condition and in addition spend less time foraging in risky locations exposed to predation. Foraging efficiency can be increased by improving food-handling skills. This increased efficiency allows greater effort to be allocated to predator detection, an activity that is mutually exclusive to foraging for a ground-feeding bird. Pheasants are highly susceptible to aerial predation from buzzards, *Buteo buteo*, and Goshawks, *Accipiter gentilis* (Kenward, Marcström & Karlbom 1981; Kenward *et al.* 2001). Therefore, we predict that birds given early exposure to a more complex diet, including live prey, will (i) develop more efficient prey handling skills; (ii) spend a shorter proportion of their time foraging, allocating more time to vigilance behaviours; and consequently (iii) survive for longer postrelease.

Increasing dietary breadth becomes paramount with the withdrawal of supplementary feeding, permitting a full transition to the wild life. An inability to identify novel food items when supplementary feeding is stopped is one of the main reasons why pheasants suffer from loss of condition during the spring (Draycott *et al.* 1998; Draycott 2002). Food discrimination and dietary preference are important learned components of foraging behaviour (Kitchener 1999). Restricting access to a wide diet due to use of homogenous commercial rearing feed early in life may inhibit individual opportunities for learning and experience. A homogenous, or narrow, diet is also likely to detrimentally affect gut development and nutrient processing. The gut is highly plastic and changes with diet (Leopold 1953; Moss 1972), and these changes affect digestive ability (Milne *et al.* 1978). Avian species are precluded from simply enlarging gut size due to the energetic costs of flight increasing disproportionally to mass (Dudley & Vermeij 1992). This trade-off between flight and digestion means that bird guts are highly

plastic. In gallinaceous birds [e.g. capercaillie (*Tetrao urogallus*) and red grouse (*Lagopus lagopus*)], individuals that eat coarser, more fibrous food have bigger guts (Moss 1972; Putaala & Hissa 1995). This has fitness consequences, with abnormal gut development suggested as one reason for poor grey partridge survival after release (Putaala & Hissa 1995). Such ability to efficiently process a broad diet, especially for omnivorous pheasants, is crucial, especially after the cessation of supplementary feeding. Therefore, we predict that birds given early exposure to a more complex diet will (i) utilize a broader diet and be less reliant on artificial supplementary feeding and (ii) develop a gut morphology better able to absorb a complex diet.

We experimentally manipulated early life diet in 2 years by supplementing uniform food with living prey and wild bird seen and fruit across different experimental groups. In the first year, we tried to isolate prey handling skills from increased dietary breadth. In the second year, we combined the two treatments. We monitored survival of individuals in the wild, and then, through experiments conducted in captivity and observations after release into the wild, we tested the four mechanisms to explain differences in survival. We predict that (i) uniform, unnatural food, even though supplying a sufficient balance of nutrients to facilitate growth and development, reduces the chances of learning discrimination skills; (ii) such a diet will result in a gastrointestinal system less able to cope with natural diet; (iii) important food-handling skills are not learned; and crucially, (iv) the improper development of such skills will affect postrelease behaviour and survival.

Materials and methods

REARING AND RELEASE INTO THE WILD

We reared and released pheasant chicks in the late spring/early summer of 2012 and 2013 on the Middleton Estate, Hampshire. The estate hosts a game shoot and employs two gamekeepers to manage the release of pheasants through habitat management, providing supplementary food and controlling predator numbers. In each year, we purchased nine hundred 1-day-old pheasants from a commercial supplier. Chicks were marked using individual numbered plastic patagial wing tags (Roxan Ltd, Selkirk, UK) and randomly allocated to treatment groups. In 2012, we applied three dietary treatments each with 10 replicate groups, with each group comprising 30 birds, thus rearing 300 birds in each treatment. In Treatment 1, a control, chicks were reared on standard rearing crumb. In Treatment 2, chicks were reared on the standard crumb with additional 5% commercial mixed seed (premium wild bird seed mix composing of wheat, cut maize, black sunflower seeds, naked oats, red dari, kibbled peanuts, yellow millet, white dari, red millet, pinhead oatmeal, canary seed, safflower seed, hempseed and raisins). In Treatment 3, chicks were reared on standard crumb with additional 1% live mealworms. In 2013, we applied two dietary treatments each with 15 replicates of 30 chicks. In Treatment 1, a control, chicks were reared on standard

rearing crumb. In Treatment 2, chicks were reared on standard chick crumb plus a combination of the supplements from 2012, with mealworms (1%) and mixed seed supplement (5%). All chick crumbs were commercial (Sportsman game feeds), age appropriate and provided *ad lib* and in excess. Water was available *ad lib*.

Each group of chicks ($n = 30$) was housed separately in a heated shed (1·3 m × 1·3 m) for the first 2 weeks and for the next 5 weeks they had access to an open grass run (1·3 m × 6·8 m) as well as the shed. Birds were in visual but not auditory isolation from other replicates throughout. To maintain stocking density, any bird that died during the rearing period was replaced by a sex-matched individual. Replacement chicks were excluded from subsequent analyses. At the age of 7 weeks, the birds from all treatments were mixed together and placed into one of two open-top release pens on the estate. Release pens typically consist of a wire mesh fence around 2 m high enclosing an extensive area of woodland into which many hundreds, occasionally several thousands, of pheasants are released (GWCT 1991). The size of pens required using this system depends on the scale of the release and adherence to good practice. The Game and Wildlife Conservation Trust recommends 1000 or so pheasants per hectare of pen (Sage & Swan 2003). Our pens measured ~1·4 Ha and 1·0 Ha and contained 360 and 540 of our birds, respectively, along with around 500 birds that had been commercially reared. The primary function of the woodland release pen is to protect the young captive-reared birds from predators, in particular foxes, whilst they get used to roosting in trees or mature shrubs (GWCT 1991) over the first week or two following release. During this period, they also provide a controlled environment for feeding and, if required, disease management (GWCT 1988, 1991). Our pens contained water and food *ad lib*. Birds could disperse at will from the pen and were free to roam and mix with other pheasants released on the estate for recreational shooting. The shooting season lasted from the beginning of October until February.

MEASURING SURVIVAL IN THE WILD

We counted the number of birds that survived the first year using three methods of recovery: (i) live birds were spotted on the estate from a distance using binoculars and identified using their patagial wing tags (2 birds); (ii) in the second shooting season, we recorded the number of year-one birds that were shot, therefore, over 17 months old and having survived a potential breeding season (19 birds); (iii) we recorded the number of year-one birds caught during an intensive trapping regime run between 14 February 2014 and 20 March 2014, meaning that any such caught birds were at least 21 months old and had survived a potential breeding season. The trapping regime used baited funnel traps to capture tagged pheasants. Traps were checked three times a day (1 bird). Because the numbers from each sampling method were small, we combined the total number of birds observed using the above methods and we used binomial tests to ask whether survival differed across rearing treatments. For birds released in 2013, we were only able to obtain survival data from birds that were shot in the 2014/2015 shooting season and thus birds that were over 18 months old (18 birds).

In order to test whether rearing condition affected adult body mass, we collected all shot birds and weighed them (Slater Super Samson spring balance – precision 5 g) within four hours of death. In addition, we weighed all birds that were caught during

the month of trapping (February–March 2014). This ensured that any differences in mass across treatment were not due to differing propensities to be shot, with lighter birds being likely to fly higher and perhaps be more likely to be shot at (Robertson, Wise & Blake 1993).

MEASURING DISPERSAL FROM THE ESTATE

Neighbouring estates and shoots were informed of the study, and released pheasants that were shot outside of the estate were returned to us. Unfortunately, the inevitable delay in returning carcasses meant that we were often unable to conduct *post-mortem* analyses on these birds. We used a chi-square test to ask whether birds that dispersed and were shot off the estate differed across rearing treatment.

MEASURING FORAGING AND VIGILANCE BEHAVIOUR IN THE WILD

In 2012, we collected continuous focal follows from 167 released pheasants, individually identified by their patagial wing tag, between 18 September 2012 and 5 November 2012. We recorded the total time observed, the time spent foraging and the number of foraging bouts they performed. A foraging bout began on the lowering of the head and neck towards to the ground and ended when the head and neck rises again. Time dedicated to a behaviour, such as vigilance, reflects the prey's perception of predation risk (Roberts 1996; Mooring *et al.* 2004). Vigilance may vary depending on protective cover (Barnard 1980; Caraco, Martindale & Pulliam 1980); therefore, we recorded the extent of protective cover as 'closed' if the focal bird was in an area offering protection from an aerial attack in the form of bushes and trees and as 'open' if there was a of such protection (e.g. open field). It was only possible to observe birds in habitats that allowed a prolonged viewing window with vegetation lower than the height of the birds. We also considered the time of day when observations were made, as this may correspond to differences in levels of hunger or exposure to predators (Rantanen *et al.* 2010) Observations were conducted from a vehicle to reduce disturbance. Between 15 August 2013 and 16 September 2013, we repeated the continuous focal follow procedure on 213 pheasants reared and released in 2013; this allowed us to collect event behaviours such as foraging time and the number of foraging bouts. At the same time, on the same focal individual, we conducted an instantaneous point sampling procedure at 30-s intervals; this allowed us to collect state behaviours, enabling us to create an activity budget.

Wild foraging percentage was calculated from data collected in the continuous focal follows conducted in 2012 and 2013 and normalized using a logit transformation: $\log(y/1-y)$ (Warton & Hui 2011) and general linear model (GLM). For vigilance likelihood, recorded using the instantaneous point sampling procedures in 2013, we used a generalized linear model (GLZM) with a binary function and a probit link function. In both models sex, early rearing environment, time of day and cover were fixed factors, including all two-way interactions. All models were visually inspected to ensure homogeneity of variance, normality of error and linearity. *Post hoc* pairwise comparisons were conducted on all significant results, and all relevant results are reported. A GLM was used to determine difference of mass between treatments controlling for the age of the bird.

EXPERIMENTALLY MEASURING FORAGING HANDLING SKILLS

In 2012, we presented 117 four-week-old chicks, randomly chosen from each treatment (mealworm = 39, mixed seed = 39, control = 39) with a food-handling test. A cricket (*Gryllus assimilus*), a novel insect that could be eaten, was tethered on a 20-cm line and concealed by a barrier connected to a pulley system. Pairs of individuals were randomly selected and placed into the arena (1·30 m × 1·30 m). Pairs were essential because preliminary work showed that singly tested pheasants were too stressed to forage. After a five-minute habituation period, the observer remotely exposed the cricket. Both birds were observed during the test. Time of detection of the cricket was recorded for both birds. Pheasants like any avian species with laterally placed eyes will first turn their head sideways to inspect food (Bischof 1988; Hodos 1993), so we used this behaviour as a measure of first detection. We then measured the time it took for the complete consumption of the cricket. We subtracted the time of first detection from the time of consumption for the analysis to obtain handling time. In 2013, we conducted the same experiment on birds reared with the mixed diet ($n = 25$) and birds from the control diet ($n = 21$). In addition to the two rearing groups, we reared 60 pheasants supplemented with dead mealworms and a sample of these ($n = 14$) and we tested these to determine whether the movement of the prey was required to enhance foraging performance, or simply a prior ingestion of an insect. This control also determined whether a simple nutritional advantage from eating mealworms led to better foraging efficiency. We used a Kruskal–Wallis test to explore differences in handling time between rearing treatments.

MEASURING DIET CHOICE IN THE WILD

In 2013, we emptied the crop of 168 shot birds and identified and quantified its contents by (i) recording the mass of all keeper-supplemented food items (wheat, barley and maize) and (ii) recording the number of nonsupplemented food types (e.g. grass, insects, galls and wild seeds). We used a Mann–Whitney *U*-test to explore differences between rearing treatment and the number of nonsupplied food types and the mass of supplementary food items found. We determined which birds were completely reliant on food provided by the gamekeeper indicated as having crops containing only supplementary feed. We also determined which birds were completely independent of gamekeeper provision indicated by a crop sample with no supplementary feed. Birds with empty crops were excluded from the analysis. We used binomial tests to ask whether rearing treatments differed in the number of pheasants with a crop content indicating complete reliance on supplementary feed or whether they differed in the number of pheasants entirely independent of supplementary feed.

MEASURING GUT MORPHOLOGY

We measured gut morphology [following methods in Leopold (1953)] of 186 birds shot in 2012. Each bird was weighed within four hours of being shot and linear gut measures (crop height, length and width; crop to gizzard, proventriculus, gizzard height, length and width, intestine length, ceca length 1, ceca length 2) were taken after removing mesenteries (for methods, see Leopold 1953). These linear measures were divided by an individual's

mean tarsus length to correct for body size. We used principle component analysis (PCA) with an oblimax rotation to collapse the 11 linear measurements, and extracted components with Eigen values >1. A MANOVA was conducted on the extracted components with the sex and rearing treatment as fixed factors.

ETHICAL NOTE

All birds were reared using commercial procedures that adhere to the DEFRA Code of Practice for the Welfare of Gamebirds Reared for Sporting Purposes (DEFRA 2009). For all behavioural testing, two birds were tested together to reduce stress, and all birds were only tested once. Released birds were attended by a gamekeeper. Once birds dispersed from the release pen, the keepers supplied supplementary feed and water, which was reduced after the shooting season (from 1st February). The birds were shot as a part of a commercial shoot and were not specifically shot for this study. The work was approved by the University of Exeter Psychology Ethics Committee and conducted under Home Office licence number PPL30/2942.

Results

SURVIVAL

In 2012, more birds reared with complex diets were detected as having survived for a year in the wild than control birds ($\chi_2^2 = 6.91$, $P = 0.032$, Fig. 1a). We detected the same pattern in 2013 when the dietary conditions were combined (binomial test, $P = 0.048$, Fig. 1b). The rearing treatment did not affect the numbers of birds that were shot ($\chi_2^2 = 1.00$, $P = 0.61$) or the numbers of birds dispersing from the estate ($\chi_2^2 = 1.51$, $P = 0.47$) during the first year after release into the wild.

FORAGING AND VIGILANCE BEHAVIOUR IN THE WILD

In 2012, individuals from the control treatment spent 12.3% longer foraging when in the wild than those reared in with supplementary mixed seed diet (*post hoc* test: $P = 0.007$) and 13.3% longer foraging than those reared with supplementary mealworms (*post hoc* test: $P = 0.001$) (GLM: treatment: $F_{2,145} = 4.24$, $P = 0.016$, Fig. 2a). Likewise, in 2013, control individuals spent 26.7% longer foraging when in the wild than birds reared with the mixed diet (GLM: treatment: $F_{2,186} = 17.90$, $P < 0.001$, Fig. 2b). Birds reared with the mixed group in 2013 spent 33.9% longer being vigilant than the control group (GZLM: treatment: $X_1 = 99.39$, $P < 0.001$, Fig. 3). These differences were not explained by time of day (2012: $F_{1,145} = 3.81$, $P = 0.053$; 2013: $F_{1,186} = 0.63$, $P = 0.43$) or level of cover in which the bird was observed (2012: $F_{1,145} = 2.93$, $P = 0.089$; 2013: $F_{1,186} = 1.78$, $P = 0.183$).

This difference in foraging time between treatments did not alter mass gain. After a period of 4–7 months in the wild, birds shot during the shooting season showed no differences in mass across treatments (2012: GLM: treatment: $F_{2,208} = 0.80$, $P = 0.45$; 2013:GLM: treatment:
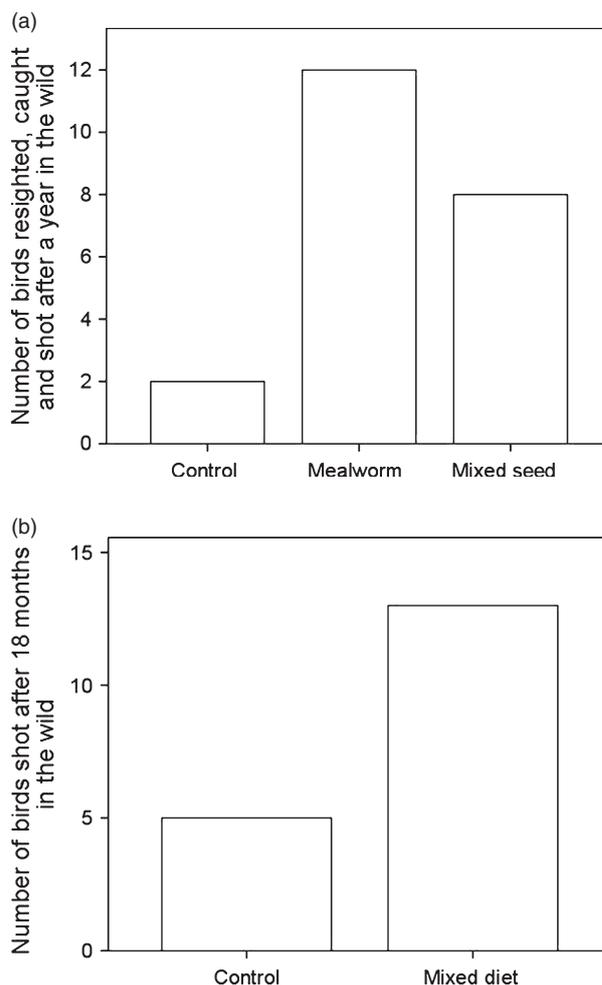
(a)

(b)

Fig. 1. The number of birds (a) reared in 2012 and resighted, shot or trapped during the following year, according to their different rearing environments and (b) reared in 2013 and shot during the 2014 shooting season after 18 months in the wild.

$F_{1,107} = 0.63$, $P = 0.43$). The birds that were caught alive during the breeding season, after a period of 8–10 months in the wild also showed no difference in mass across treatments (GLM: treatment: $F_{1,27} = 0.01$, $P = 0.91$).

FOOD-HANDLING SKILLS

In 2012, birds reared with mealworms were more than twice as fast at catching and eating the tethered crickets after detection than those reared with supplementary mixed seed (*post hoc* test: $P = 0.003$) or the controlled diets (*post hoc* test: $P = 0.003$) (Kruskal–Wallis: $H(2) = 14.59$, $P = 0.01$, Fig. 4a). There was no difference in the amount of time it took to detect the cricket between treatments (Kruskal–Wallis: $H(2) = 1.02$, $P = 0.60$). In 2013, we found that birds reared with live mealworms were quicker to eat the cricket after detection than both the birds reared with dead mealworms (*post hoc*: $P = 0.001$) and those reared with the controlled diet (*post hoc*: $P = 0.004$). Birds reared with dead mealworms
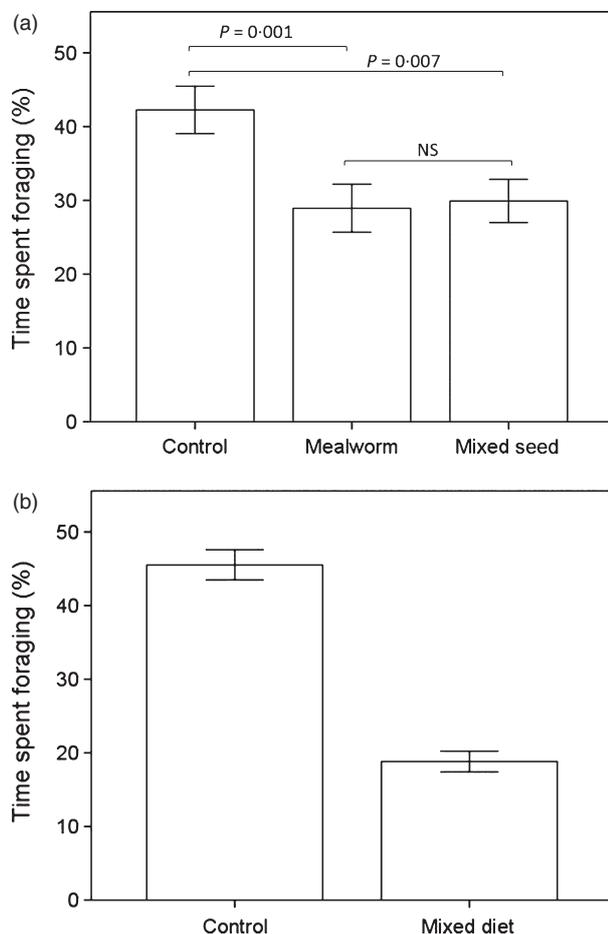
Fig. 2. The mean percentage of time spent foraging in the wild by a bird reared under differing environments in (a) 2012 and (b) 2013. Error bars indicate ±1 SE. Significance values of post hoc tests are given.
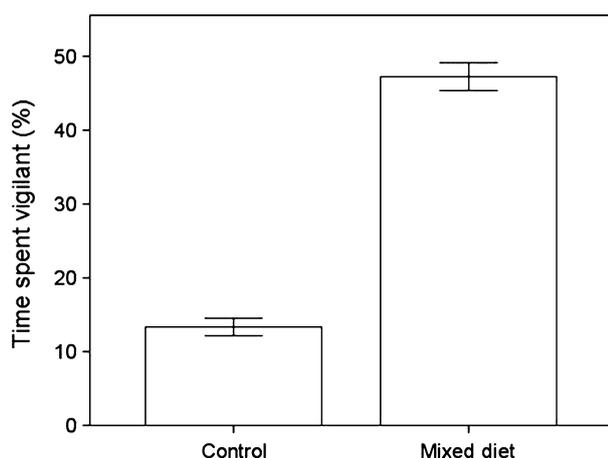

Fig. 3. The mean percentage of time spent being vigilant in the wild by a bird reared under differing environments in 2013. Error bars indicate ±1 SE.

showed no difference in their ability to consume a cricket after detection than birds reared without mealworms (*post hoc* test; $P = 0.39$) (Kruskal–Wallis: $H(2) = 14.51$, $P = 0.001$, Fig. 4b).

DIET CHOICE

The mass of supplemented food (maize, wheat and barley) found in the crop of birds shot in 2013 did not differ with their rearing treatment ($U_{168} = -1.14$, $P = 0.25$). However, the birds reared with the mixed diets had higher numbers of nonsupplied food types in their crop compared to birds reared with the control diets ($U_{168} = 2.51$, $P = 0.012$, Fig. 5). There were disproportionately more birds reared with the control diet completely reliant on supplementary food items than birds reared with the mixed treatments (Binomial Test, $P = 0.007$). Birds from the mixed group tended to be more likely to be completely independent of keeper provision than the birds reared in the control environment, (Binomial Test, $P = 0.072$).

GUT MORPHOLOGY

We extracted two principle components scores from the 11 measures of the digestive system from birds reared in 2012. Component one explained 36% of the variation and was strongly associated with intestine length, caecum 1
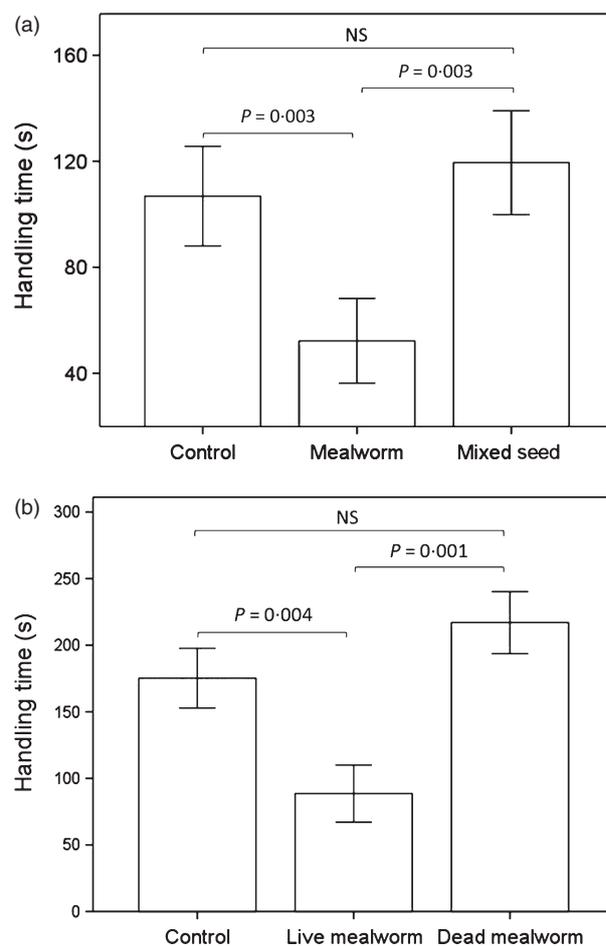

Fig. 4. Time taken for a focal chick reared with one of three diets to eat a live cricket once it had been detected in (a) 2012 and (b) 2013. Error bars indicate ±1 SE.
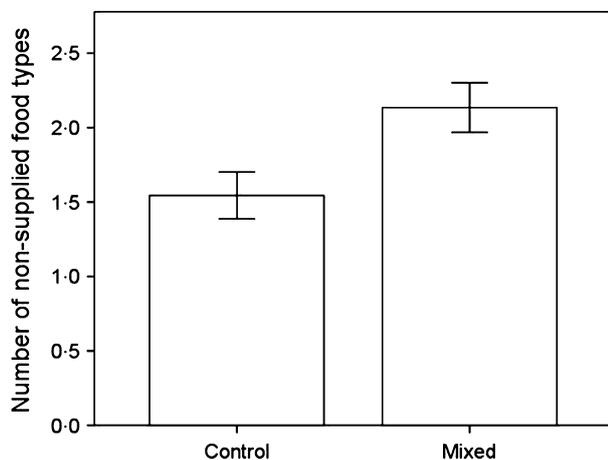
Fig. 5. The mean number of different types of nonsupplied food items identified in the crops of birds shot during the first shooting season. Error bars indicate ±1 SE.

Fig. 6. Mean PC1 score representing hind gut morphology for birds reared with either controlled or mixed diet. A low value indicates a short hind gut and high values indicates a large hind gut. Error bars indicate ±1 SE.

length and caecum 2 length. Therefore, a high PC1 score indicates an elongated hind gut. The second component explained a further 15% of the total variation with a high loading from crop height, width and depth. Therefore, a high PC2 score indicates a large crop size. Birds reared on control diets had relatively longer hind guts (PC1) than those reared on enriched diets ($F_{2,185}$ = 3·54, P = 0·031, Fig. 6). Mealworms and mixed seed birds did not differ in hind gut length (PC1: *post hoc* test P = 0·30), but controls differ from birds reared with mealworms (P < 0·001) and to a lesser extent those reared with mixed seeds (P = 0·13). Sexes did not differ in their relative hind gut lengths ($F_{1,185}$ = 0·41, P = 0·52). There was no overall effect of treatment on the relative size of the crop (PC2: $F_{2,185}$ = 2·10, P = 0·13).

Discussion

An enriched diet early in life increased the survival of released pheasants. After a year living in the wild, we detected 2·6–5 times more birds that were reared with an enriched diet compared to birds reared under control conditions. These apparently dramatic improvements in survival should be treated with some caution, given the relatively small sample sizes that we could collect in each year. However, our replication of the finding across two separate years with distinct cohorts of released birds gives us confidence in the existence of the effect, even if not the magnitude. We do not believe that the most common sampling technique – recovery of shot birds – was biased to produce such results: we did not detect that likelihood of dispersing off the estate and so being less likely to be shot differed with rearing diet, nor did we detect mass differences across rearing treatments in the birds that were shot which may affect their flying height and hence propensity to be shot at. Instead, we believe that this increased survival may be explained by behavioural and physiological characteristics provoked by the more
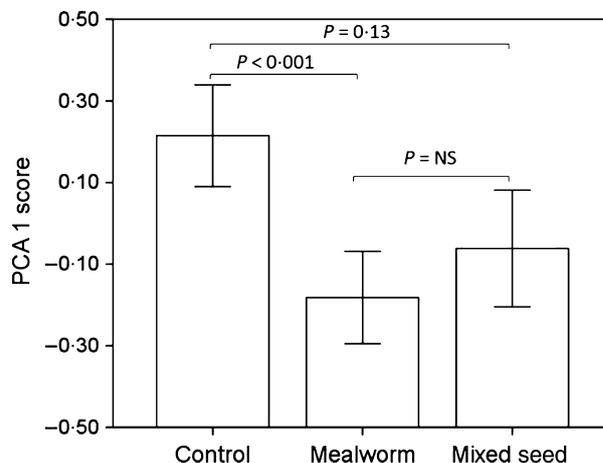
complex diet provided during their early rearing environment. A diverse diet, including live prey and a range of seeds and fruits, increased the handling speed of adults, resulting in more efficient foraging so that more time could be spent being vigilant. These adults also had a wider diet and were less reliant on supplemented food. This may have been facilitated by a more efficient digestive system. In both years of the study, birds reared with complex diets spent less time foraging in the wild than birds reared with the control diet, yet did not weigh any less at death, suggesting that they were more efficient in their foraging behaviour. This increased efficiency can have three positive influences on survival. First, spending less time foraging may reduce the energetic costs associated with foraging (Burrows & Hughes 1991). Secondly, lower foraging time reduces the time exposed to predators (Lima 1985; Guillemain *et al.* 2007). Risk of exposure to predators is particularly high for galliforms as they forage with their head and eyes directed towards the ground, and therefore, the probability of detecting a predator is reduced (Pulliam 1973; Fernández-Juricic *et al.* 2011). Poor antipredator behaviour has also been observed in hand-reared whooping cranes (*Grus americana*), compared to the more naturalistic parent-reared birds (Kreger *et al.* 2005). One reason for the poor success of released grey partridge is that they do not behave adaptively in terms of vigilance and predation, determined by poor group and individual level vigilance compared to wild conspecifics (Watson, Aebischer & Cresswell 2007; Rantanen *et al.* 2010).Thirdly, spending less time foraging allows for the performance of other important behaviours such as being vigilant (Lima 1987). In our study, birds reared with complex diets were more vigilant than birds reared with controlled diets.

Increased foraging efficiency, exhibited by birds reared with an enriched diet, could be explained by better handling skills. Pheasants exposed to live prey from early in

life were no more likely to detect a novel live prey than control groups, but were about twice as fast to eat it. Insects are an important part of pheasant diet during the autumn (Lachlan & Bray 1973). Birds required the provision of a living, moving insect to learn the appropriate foraging technique. The provision of a dead insect did not improve the pheasant's ability to consume a novel insect. This also suggests that the simple nutritional benefit provided by the provision of mealworms, either alive or dead, during development did not affect the more general ability to forage more efficiently during the tests.

There was no difference between treatments in the masses of pheasants when shot, or those that we trapped. This confirms two important issues associated with manipulation in behaviour. First, the more efficient foragers, in this case the birds reared with complex diets, did not simply use their new ability to eat more and increase their mass; instead they allocated the time to other behaviours including vigilance. Secondly, the higher vigilance adopted by birds reared with complex diets was not attributable to the starvation–predation hypothesis (Lind & Cresswell 2005; Watson, Aebischer & Cresswell 2007), as we found birds were able to forage efficiently, maintaining their vigilance levels whilst maintaining their mass gain.

Birds reared with a complex diet had greater dietary diversity after release than control birds. They were also less reliant on artificially provisioned supplementary food. Preferences for, and discrimination of, natural food sources is not innate but is shaped during early life. It is important to note that the crop samples were taken during the shooting season when the birds still had access to supplementary feed and that across rearing treatments the mass of supplementary feed did not differ. Therefore, we expected to see large quantities of keeper-supplied food in the diet of all birds. The ability and propensity to utilize natural resources, even when supplementary feeding was still occurring, could explain why we saw equal numbers of birds across treatments at the end of the shooting season, but why 4 months later we observed substantially more pheasants reared with complex diets surviving after the cessation of supplementary feeding. The ability to discriminate and choose natural food items is essential. Food discrimination may be learnt socially by local enhancement. White tailed ptarmigan (*Lagopus leucurus*) and domestic chicken (*Gallus gallus*) mothers will provide unique vocalization to lure chicks to profitable food sources (Nicol & Pope 1996; Nicol 2004; Allen & Clarke 2005). The ability to learn foraging skills from parents was suggested to be one of the primary reasons for increased survival of parent-reared sandhill cranes (*Grus Canadensis*) compared to hand-reared individuals (Ellis *et al.* 2000). It is not just the ability to detect a variety of food items which could explain the increased foraging efficiency adopted by birds reared with the complex diets, and they may have developed a wider set of

handling skills necessary to obtain and ingest novel fruits and seed, essential in omnivorous pheasants. Although pheasants reared with mixed seed and fruit in 2012 did not differ from the control group in the time it took to eat a novel insect, these birds may utilize other skills that they learnt from their own rearing environment that improved their foraging efficiency upon release. Handling of food items, especially live prey, commonly improves with experience (Thornton 2008), and the development of handling techniques is essential for survival and fitness (Thornton 2008). Captive-bred black-footed ferrets (*Mustela nigripes*) exposed to live prey are found to be more effective killers when adults than those fed dead prey (Miller *et al.* 1992; Vargas & Anderson 1999). Bank voles reared in captivity were unable to open nuts that were easily opened by their wild conspecifics (Mathews *et al.* 2005). Therefore, we suspect that birds reared with complex diets were both more likely to identify and sample novel food types and be better able to process them for ingestion.

We detected morphological as well as behavioural differences according to early rearing environments. Birds reared with complex diets had shorter hind guts. This suggests that they have been consuming a high-energy and low-fibre diet for a period of time prior to being shot (Moss 1972; Putaala & Hissa 1995; Liukkonen-Anttila, Saartoala & Hissa 2000). Whilst we would expect gut morphologies to differ prior to release when we had control over intake, the plastic nature of the avian gastrointestinal system suggests that these pheasants continued to find and consume a high-energy and low-nutrient diet after release. If the complex diet birds were restricted in their diet to the same options as those of the control birds, then we would expect that after 3–6 months in the wild the gut morphologies would converge (Redig 1989). However, birds reared with complex diets also had greater nonsupplied food types, such as insects and seeds, identified in the crop analyses compared to birds reared with controlled diets, suggesting that they were utilizing a higher energy and lower fibre diet to maintain the gut morphology. This is important as poor gut development is suspected to be a reason why birds do not maintain body condition after the cessation of supplementary feeding (Draycott *et al.* 1998; Draycott 2002). The increased size of the hind gut in control birds may also indirectly affect survival. Larger guts reduce an individual's ability to fly (Dudley & Vermeij 1992). Therefore, a trade-off is required between maximum digestion and mobility. Here, our complex diet has not only created a gut system, likely better able to cope with the more naturalistic diet that is forced on the birds after the cessation of supplementary feeding, but is also about 5% smaller, likely increasing flight efficiency and hence predator avoidance.

We conclude that in pheasants, diet, foraging behaviour, gut morphology and digestive capabilities all work together as one nutritional complex (Thomas 1987) and

that a simple manipulation of diet during early development in captivity can have a cascading effect on individual survival. However, in captive rearing environments, diet is typically restricted with many intensive rearing systems using processed feed (Liukkonen-Anttila, Putaala & Hissa 2002), which is homogenous in form and in excess (Villalba, Provenza & Manteca 2010). This food is nutritionally balanced but may not give the animal the diverse diet that it would have if it was foraging in the wild. For instance, pheasant chicks in the wild are omnivorous, feeding almost entirely on insects for the first few weeks of life and then extending their diet to include seed and plant material (Dalke 1937; Warner 1979). In captivity, prereleased chicks are fed with commercial pellet for the first 8 weeks of life (Hill & Robertson 1988). The composition of the feed provided will mean that upon release animals will show an obvious differences in condition compared to wild animals (Putaala & Hissa 1995; Rabin 2003), being heavier and in better condition following a tailored commercial diet. However, exclusive use of artificial feed may retard the development of important foraging mechanisms. Thus releasing animals that 'look' like a wild individual (Putaala & Hissa 1995; Rabin 2003) does not mean those animals have the behavioural and physiological characteristics to survive. For instance, a balanced but homogenous diet, even if nutritionally analogous to the wild, will produce an animal with a body condition comparative to its wild counterparts, but it will not have provided the necessary learning of food discrimination and handling that young in the wild experience. Pheasants are currently released in extremely high numbers to combat the poor survival after release. Therefore, rearing a bird with the ability to cope with a wild diet, leading to the subsequent improvements in survival that we detected may mean that far fewer pheasants need to be released each year whilst still maintaining economically viable levels for shooting. A reduction in the 35 million pheasants currently released in the United Kingdom would have financial, ethical and environmental benefits for both the shooting industry and natural environment as a whole (Sage, Ludolf & Robertson 2005). These results provide strong evidence for the need for careful consideration of natural rearing conditions within captive populations prior to release if we want to ensure that captive individuals have adaptive behavioural and physiological characteristics to cope with the wild stressors and survive postrelease.

Acknowledgements

Data accessibility

Data available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.56b32 (Whiteside, Sage & Madden 2015).

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