



## Low heritability in tool use skills in a wild vulture population



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Tool use is widespread among animals and has been under intense study due to its prominence in human society and evolution. A lack of detailed genetic information for wild populations has perpetuated assumptions regarding associations between individual differences in tool use and cognition and learning processes. However, captive birds and mammals can use tools in the absence of opportunities for social learning, indicating a genetic basis. Here, we used animal models and relatedness analysis to disentangle the role played by genetics and learning in tool use in an insular population of a long-lived vulture, *Neophron percnopterus*. Our results show a low heritability in this behaviour, perhaps because of the low variability observed among birds. However, not all individuals used stones to break eggs, and those that did so behaved consistently. Importantly, there was no evidence of learning at the timescale considered. Our results suggest that repeatability in tool use within individuals may indicate a link with some personality traits, with strong evolutionary and ecological consequences.

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Animal tool use has been the subject of intense debate ever since it was first observed, due to its prominence in human society and evolution. Early on, scientists assumed that tool use in animals had the same cognitive basis as tool use in humans. However, as more examples were discovered across phyla, tool use came to be regarded as just another adaptation to ecological problems, or occasionally an outcome of redirected 'emotional' responses or simple trial-and-error learning (Hansell, 2005 and references therein). Difficulties in obtaining detailed genetic information from wild populations have favoured the idea that individual differences in tool use are related to cognition and are due to social learning. For example, tool use among bottlenose dolphins, *Tursiops* sp., is understood to be a consequence of cultural transmission instead of a heritable trait transmitted from parents to offspring (Krützen et al., 2005). However, experimental studies with woodpecker finches, *Cactospiza pallida*, and New Caledonian crows, *Corvus moneduloides*, showed tool use in birds reared with no opportunity to learn socially (Kenward, Weir, Rutz, & Kacelnik, 2005; Tebbich, Taborsky, Fessl, & Blomqvist, 2001), pointing to a genetic basis.

Other studies on primates suggest that complex manipulative behaviours (such as motor skills and handedness) are heritable (Hopkins, Reamer, Mareno, & Schapiro, 2015) or derive from genetic predispositions and individual learning (Menzel, Fowler, Tennie, & Call, 2013; Tennie, Hedwig, Call, & Tomasello, 2008). Thus, the debate about the relative importance of nurture (environment) and nature (genes) in the development of behavioural traits across animal taxa and the role played by internal and external (e.g. physiological, motivational or ecological) stimuli (Tennie, Call, & Tomasello, 2009) is still open.

Here, we performed an Island test to quantify individual variation in tool use, the heritability of this behaviour and the importance of learning in the acquisition of this skill. We used a long-term monitored population of Egyptian vultures, *Neophron percnopterus*, as a study model. The Egyptian vulture is a true tool user (Tebich et al., 2001), which drops stones onto ostrich, *Struthio camelus*, eggs to obtain egg yolk (Lawick-Goodall, & van Lawick, 1966). We combined experimental and genetic data through relatedness analyses and animal models in a sedentary pedigreed population that lost its contact with ostriches 2500 years ago (Agudo, Rico, Vilà, Hiraldo, & Donazar, 2010). To our knowledge, this is the first study to explore tool manipulation in a long-lived species, other than apes, using information on an extensively

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monitored wild population. Owing to the observational nature of our study, we did not differentiate social from individual learning. Thus, we defined learning as the improvement in an individual's ability (here, tool use) through time.

## METHODS

### *Study Species and Population*

The Egyptian vulture is a long-lived, medium-sized scavenger widely distributed throughout arid Old World regions, with insular populations in the Mediterranean and Arabian Seas and the Atlantic Ocean (Agudo et al., 2008). In the latter region, the largest population survives in the eastern islands of the Canary archipelago. Birds breeding in continental Europe and wintering in the African Sahel (Carrete et al., 2013), where the species' range has historically overlapped with that of ostriches, developed the ability to use stones to break ostrich eggs. In contrast, Egyptian vultures on the Canary archipelago are sedentary and a different subspecies founded from a few vagrant birds around 2500 years ago (less than 200 generations; Agudo et al., 2010). These insular birds have had no contact with ostriches (or their eggs) for millennia, constituting an ideal situation to perform an Island test (Tennie & Hedwig, 2009; Tennie, Braun, Premo, & McPherron, 2016).

From 1998 to 2009, the population of Fuerteventura has been intensively monitored. During this period, 175 fledglings were captured at nests and 82 immature and adult birds were trapped by cannon netting. All birds were marked using both metal and plastic rings with an individual alphanumeric code, and released after blood samples (5 ml) were taken. Blood samples were preserved in absolute ethanol and kept at 4 °C until processed in the laboratory. Adult and immature birds were aged by plumage features, sexed by molecular markers (Fridolfsson & Ellegren, 1999) and genotyped at 22 microsatellites (Gautschi, Tenzer, Müller, & Schmid, 2000; Agudo et al., 2008).

### *Behavioural Experiment*

Experiments were carried out during the nonbreeding seasons from September 2006 to January 2008, when most of the population gathers at a feeding area in the centre of the island (García-Heras, Cortés-Avizanda, & Donazar, 2013). There, we placed an ostrich egg twice a week and, to avoid changes in behaviours linked to differences in stone availability, we cleaned the area and placed 15 stones of similar size near the egg. Every session was video-recorded and watched in the laboratory to register the identity of the birds present in a 50 m radius around the egg every 15 min and of those approaching the egg and picking up stones to throw. We identified over successive sessions those individuals that used stones and those that did not. Observations took place when there was no food in the feeding area to avoid disturbances from other feeding stimuli and were stopped when birds lost interest and abandoned the area.

### *Heritability Estimates*

Estimates of heritability should ideally rely on complete pedigrees, a situation rarely found in studies of wild populations. Nevertheless, the application of molecular markers can help by estimating pairwise relatedness using individual genotypes. Here, we used these two complementary approaches. First, we estimated heritability in tool manipulation through animal models by using a Bayesian Markov chain Monte Carlo technique implemented in the MCMCglmm package in R (Hadfield, 2010). MCMCglmm separates phenotypic variance into additive ( $V_A$ ) and nonadditive ( $V_{NA}$ ; i.e.

dominance effects, epistasis, etc.) genetic variance, simultaneously considering any potentially confounding effects. We assessed heritability as  $V_A/V_P$ , where  $V_P$  is the total phenotypic variance in tool use calculated as  $V_A + V_R$  (i.e. the residual variance, including nonadditive genetic and environmental variances).  $V_A$  and  $V_P$  were inferred from the pedigree information, also considering the effect of individual age and sex (fixed effects). The pedigree was built using information from 141 individual genotypes available from previous studies (Agudo et al., 2010, 2011). These were used to make a parentage reconstruction through maximum-likelihood estimates of pairwise relatedness coefficients and genealogical relationships (ML-relate software; Kalinowski, Wagner, & Taper, 2006). As extrapair paternity is extremely rare in this population, the pedigree was completed using genetic and social information incorporating 139 ringed birds and 13 birds identified by plumage or physical characteristics. Most of these birds belonged to 14 families formed by more than one pair of parents and their offspring. We also included 'individual' in models as a random term to account for the nonindependence of behaviours performed by a single individual and to estimate the variance in tool use among individuals for any reason other than additive genetic effects (e.g. environmental or maternal effects). Repeatability ( $r$ ) and heritability ( $h^2$ ) in tool use were calculated as  $r = \sigma_{\text{individual}} / (\sigma_{\text{individual}} + \sigma_{\text{animal}} + \sigma_{\text{units}} + 1)$  and  $h^2 = \sigma_{\text{animal}} / (\sigma_{\text{individual}} + \sigma_{\text{animal}} + \sigma_{\text{units}} + 1)$ . We also tested whether tool use could be learned (i.e. the probability of tool use increases over time) by including sessions as a covariate in the models.

Models were run with priors for the random variances set to 1, and a degree of belief  $N = 1$ . Residual variance (VR) was fixed at 10 to optimize mixing of the chains and reduced autocorrelations. Estimates were insensitive to the choice of priors (prior variances range 0.01–100). Parameter expansion was used to avoid poor mixing if variance component estimates were close to zero. All models were run for 1 000 000 iterations, preceded by a burn-in of 10 000 iterations. Estimates of parameters were stored every 100th iteration to reduce autocorrelation. We tested the statistical support of the fixed effects (sex, age and session) by evaluating whether their posterior distributions (95% credible interval) overlapped zero.

We also inferred the relatedness among 132 individuals using their genotypes to evaluate relatedness in tool use for individuals that were not included in any of the 14 families mentioned above. We estimated relatedness between dyads of individuals (package related in R; Pew, Muir, Wang, & Frasier, 2014) using Wang's coefficient (Wang, 2002) because it showed the highest correlation coefficient ( $r = 0.80$ ) between observed and expected relatedness for each of the seven tested estimators. Negative relatedness values of this estimator are due to sampling errors linked to the use of individuals across generations as a reference population, and do not reveal any biological meaning (Wang, 2014). We tested whether tool manipulation is a heritable trait by grouping individuals that manipulated stones ( $N = 29$ ) and those that did not ( $N = 103$ ). We hypothesized that individuals displaying an inherited behaviour ( $r_M$ ) would be more related than if they were a random group of individuals that did not manipulate stones ( $r_{NM}$ ). We compared the average relatedness within groups ( $r_M$  and  $r_{NM}$ ) with the distribution of relatedness values simulated after randomly shuffling individuals between groups (grouprel function).

## RESULTS

### *Behavioural Experiment*

We recorded 1627 different observations corresponding to 152 different individuals. Most of the individuals ( $N = 120$ ) never used

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