THE CONDOR
Ornithological Applications
AmericanOrnithology.org

Volume 117, 2015, pp. 624–628
DOI: 10.1650/CONDOR-15-70.1

COMMENTARY

Can interrupting parent–offspring cultural transmission be beneficial? The case of Whooping Crane reintroduction

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Submitted April 24, 2015; Accepted July 24, 2015; Published October 21, 2015

ABSTRACT

Inheriting behavioral patterns culturally (i.e. by learning from parents) rather than genetically is considered an integral part of individual development for many bird and mammal species. I discuss the possibility that in some cases, particularly when only heavily modified habitat remains available, such transmission might have a negative effect on the individual's adaptability and chances of survival. Instead, animals deprived of normal parental care may be better suited for survival in novel environments. I describe this possible scenario with captive-reared Whooping Cranes (*Grus americana*) released in southwestern Louisiana, primarily in the context of human-modified habitats used by this reintroduced population. Captive-rearing techniques based on this approach may be beneficial for other threatened species, particularly those that have little or no nonmodified habitat left and are amenable to alternative habitats if cultural transmission is interrupted.

Keywords: adaptability, behavioral flexibility, cultural inheritance, endangered species, *Grus americana*, modified habitats, novel behavior, reintroduction

¿Puede ser beneficiosa la interrupción de la transmisión cultural entre padres e hijos? El caso de la reintroducción de *Grus americana*.

RESUMEN

Se considera que la herencia de patrones culturales de comportamiento (i.e. aprendiendo de los padres) más que una cuestión genética es una parte integral del desarrollo del individuo para muchas especies de aves y mamíferos. Aquí analizo la posibilidad de que en algunos casos, particularmente cuando solo queda disponible hábitat altamente modificado, esta transmisión podría tener un efecto negativo en la adaptabilidad del individuo y en las probabilidades de supervivencia. En cambio, los animales desprovistos del cuidado parental normal podrían estar mejor preparados para sobrevivir en nuevos ambientes. Describo este posible escenario con individuos criados en cautiverio de *Grus americana* y liberados en el sudoeste de Luisiana, principalmente en hábitats modificados por el hombre usados por esta población reintroducida. Las técnicas de cría en cautiverio basadas en este enfoque pueden ser beneficiosas para otras especies amenazadas, particularmente para aquellas que tienen poco o no tienen hábitat no modificado remanente y que son flexibles a hábitats alternativos si se interrumpe la transmisión cultural.

Palabras clave: adaptabilidad, especies en peligro, flexibilidad comportamental, *Grus americana*, hábitats modificados, herencia cultural, nuevo comportamiento, reintroducción

> The increasing rate and complexity of global change, including habitat loss, species declines, biological invasions and climate change suggest entry into an age of "ecological surprises" where management solutions based on historical precedent may not always be adequate for future biodiversity conservation needs. (IUCN/SSC 2013)

Cultural inheritance of behavior, or behaviors passed from adults to offspring via learning rather than genetically, has been the focus of much research in recent years. Numerous field and theoretical studies have underlined its importance for survival (see, e.g., Cavalli-Sforza and Feldman 1981, Jochim 1981). Conservation workers have made heroic efforts trying to reproduce this mechanism when returning orphaned animals (particularly apes and large carnivores) to the wild (Pazhetnov and Pazhetnov 2005, Hayward and Somers 2009, Russon 2009). The benefits of parental care and cultural transmission of knowledge are thus well known. But is it possible that

FIGURE 1. A reintroduced Whooping Crane (*Grus americana*) in dense floodplain forest in Louisiana.

interrupting this mechanism could be beneficial for some animals?

The first suggestion to this effect was made by Russon (2009), who noted higher diversity of tool use in orangutans (*Pongo* spp.) that had been orphaned, rehabilitated, and released into the wild than in fully wild ones; orphan orangutans that lacked maternal guidance in traditional tool use invented their own tools. Indeed, animals that have been orphaned and subjected to extensive human contact often show novel forms of behavior. Hand-raised crows and ravens (*Corvus* spp.) are particularly adept at learning new ways of procuring food in urban landscapes (Marzluff and Angell 2013). But in many of these cases, it is probably the unusual teaching or conditioning by humans, rather than the lack of parental guidance per se, that is responsible for novel behaviors.

One particular area of importance for animals' survival in the modern world is habitat flexibility—or, more precisely, the ability to thrive in human-modified habitats despite high levels of disturbance and other negative factors. Lack of flexibility in habitat choice might lead animals to habitats that satisfy their evolved habitat preferences but are no longer sufficient for survival, or to ignore habitats that can be successfully used. Dwernychuk and Boag (1972) called the former situation an "ecological trap," and Patten and Kelly (2010) called the latter situation a "perceptual trap." These and other cases of fitness loss and potential extinction due to outdated behavioral patterns are collectively known as "evolutionary traps" (Schlaepfer et al. 2002).

Can interrupting cultural transmission lead to higher habitat flexibility and help a population get out of such an evolutionary trap? This seems to be the case for captive-reared cranes (*Grus* spp.). Whooping Cranes (*G. americana*) currently exist in a number of populations, or "flocks," but only one of them, the Aransas-Wood Buffalo population (AWBP), is derived exclusively from wild, parent-reared individuals; all others result from reintroductions of captive-reared birds, mostly within the supposed former range of the species (as in Allen 1952). The captive-raised birds are reared by costume-wearing humans or by tame captive adults (BirdLife International 2012b), so these birds cannot inherit habitat preferences and natural behaviors through cultural transmission. Whatever habitat preferences they express must be either innate or developed by individual experience.

All historical records and recent observations (Allen 1952, Timoney 1999, Austin and Richert 2005) show that the AWBP Whooping Cranes have relatively narrow habitat preferences. In summer they inhabit large open wetlands of a particular type, surrounded by boreal forests. In winter they live in extensive wetlands with good visibility, occasionally move to drier grasslands or croplands, and only rarely use small ponds surrounded by open woodland. Historically, wild Whooping Cranes in Louisiana occurred almost exclusively in wet, partially flooded prairies (Allen 1952). Reintroduced cranes from captive populations do not show such narrow habitat use. Unlike wild, parent-raised AWBP birds, Whooping Cranes in Florida use a wide variety of habitats, including pine forests, pastures, fields of varying size, and suburbia (Fondow 2013). Even more spectacular is the diversity of habitats used by Whooping Cranes in Louisiana: They use natural marshes, agricultural fields, pastures, vacant lots overgrown with tall grass, shores of suburban lakes and reservoirs, small forest clearings, and even dense floodplain forests (Louisiana Department of Wildlife and Fisheries 2014, V. Dinets personal observation; Figure 1). Whooping Cranes in Florida and Louisiana are descendants of the AWBP population, so their behavioral differences cannot be due to genetic variation. Instead, their broader habitat flexibility must reflect their individual experience: Rather than accompanying their parents for the first 9 or more months of their life, they were raised in an artificial environment and released into the wild, unaccompanied by experienced birds. Some of them are raised by captive birds rather than by humans, but their parents don't have the opportunity to teach them which habitats to use, and there are no experienced conspecifics available to provide cues. The resulting flexibility allows them to utilize seasonally abundant food resources such as reptiles and amphibians basking on dikes that separate rice fields, or masses of froglets and tadpoles in flooded forests (Dinets 2015).

Is this behavioral flexibility beneficial? That is not a simple question. When colonizing novel habitats, birds can suffer increased mortality due to poaching (particularly in agricultural landscapes, as has occurred repeatedly in Whooping Cranes in Louisiana; see Louisiana Department of Wildlife and Fisheries 2014) or predation (particularly in forested habitats). Conversely, the ability to colonize human-modified habitats might lead to rapid population growth, as in the case of Florida Sandhill Cranes (*G. canadensis pratensis*; Archibald and Meine 1996), or even be the last hope for a declining population, as in the case of White-naped Cranes (*G. vipio*) and Hooded Cranes (*G. monachus*) wintering in agricultural fields in Japan (Archibald and Meine 1996, Harris and Mirande 2013). So it is possible that captive-raised cranes may have higher chances of prospering in the modern world and starting "new" populations without cultural inheritance than those raised by parent cranes. Indeed, this is the case for Mississippi Sandhill Cranes (*G. c. pulla*), which now exist as a single small population inhabiting highly modified habitats and remnant pine savannas managed for the cranes' benefit. In this population, hand-reared juveniles have higher survival rates than parent-raised or wild-born juveniles (Ellis et al. 2000), although this hasn't yet resulted in making the population self-sustaining. Rearing birds that are less prone to human disturbance than parent-raised wild ones is now used as an alternative approach to raising the numbers of Red-crowned Cranes (*G. japonica*) in Russia and China, although the effectiveness of this method is not yet clear (O. Smirensky personal communication). And the reintroduced cranes in Louisiana also appear to be faring well: So far, their mortality is lower than that of AWBP birds of the same age (Gil-Weir et al. 2012, Butler et al. 2014, Harrell 2014, Louisiana Department of Wildlife and Fisheries 2014, Stehn and Haralson-Strobel 2014), even if migration-related losses in AWBP birds are not counted.

It is possible that some synanthropic populations of other birds and mammals originate from individuals deprived of parental guidance. This is certainly the case for urban populations of the Peregrine Falcon (*Falco peregrinus*) in the eastern United States, which have all been founded by captive-raised birds (Cade et al. 1996). The booming population of Borneo orangutans (*P. pygmaeus*) in Tajung Puting National Park, Indonesia, is a mix of rehabilitated and fully wild animals; the latter have learned from the former to tolerate human disturbance and utilize supplemental food (Yeager 1997). An urban population of normally shy pine martens (*Martes martes*) in Kozhym, Russia, originated with a litter of orphaned and subsequently hand-raised individuals (M. Molyukov personal communication).

Countless species now face the choice between adaptation to new habitats and extinction–extirpation, so interrupting parent–offspring cultural transmission might prove to be a useful conservation tool, particularly for bird species that are currently restricted to remote wilderness but potentially capable of colonizing city parks, suburban forests, and other heavily modified habitats. A good example of such species is the Oriental Stork (*Ciconia boyciana*). Although ecologically very similar to the White Stork (*C. alba*), which is abundant in many parts of Europe and nests almost exclusively in human settlements, this bird is endangered, mostly because of its extreme sensitivity to human disturbance (Hancock and Kushan 1992). It seems logical to attempt establishing populations of the Oriental Stork and other wary species in urban or agricultural landscapes using captive-raised birds without culturally inherited behaviors.

There are already indications that tame captive-raised birds can be surprisingly successful in human-modified environments. A reintroduction of captive-bred Oriental White Storks in an agricultural area in Japan has succeeded, with remarkably high survival rates (Ezaki et al. 2013). Reintroduced captive-raised Crested Ibises (*Nipponia nippon*) show higher behavioral plasticity than wild ones and comparably high survival rates (Nagata and Yamagishi 2013, Huo et al. 2014, Liu et al. 2015). Yet another example is the establishment of reintroduced Northern Bald Ibises (*Geronticus eremita*) in Spain, where captive-raised birds nest on a small roadside cliff and show no signs of distress when closely approached by humans (Molina et al. 2013, V. Dinets personal observation). This may complement the traditional approach of raising birds in ways that discourage tolerance of humans and then releasing them in remote locations.

There are, of course, numerous potential problems to consider. Lacking parental knowledge might make survival impossible, as in the case of captive-bred Thick-billed Parrots (*Rhynchopsitta pachyrhyncha*) unsuccessfully reintroduced in Arizona (Snyder et al. 1994), or create the need for risky and labor-intensive teaching by humans, as in the case of Whooping Cranes reintroduced to Wisconsin and taught to migrate to Florida (Clegg et al. 1997). New animals might be unwelcome in populated areas if they become or are perceived as pests, dangerous animals, or sources of disturbance, and this might endanger the whole reintroduction effort. For example, an attempt to introduce hand-raised large carnivores with no natural fear of humans into a populated area might have disastrous consequences. Note, however, that even for large carnivores, tameness might be beneficial: The population of Iberian lynx (*Lynx pardinus*) in Sierra de Andujar, Spain, has recently started rapidly growing after decades of decline (Simon et al. 2012), despite the fact that many of the animals are amazingly tame (V. Dinets personal observation); according to local landowners, this tameness helps improve the animal's public image and attract tourists. Thriving urban populations of leopards (*Panthera pardus*) in India are another well-known example: One such population, recently boosted by translocations from other areas, exists within the megalopolis of

Mumbai and is generally tolerated, despite occasional predation on humans (Ghosal 2012).

Animals that live in heavily modified habitats can be expected to face numerous additional risks and suffer higher mortality, as shown for Florida Sandhill Cranes (*G. c. pratensis*; Toland 1999) and, possibly, Florida Scrub-Jays (*Aphelocoma coerulescens*; Thaxton and Hingtgen 1996, Breininjer 1999; but see Bowman and Woolfenden 2001). However, despite these risks, it is not uncommon for animals in modified habitats to fare better than those in "natural" ones. For example, reintroduced New Zealand Falcons (*F. novaeseelandiae*) have higher breeding success in agricultural landscapes than in forested ones (Kross et al. 2012). Escapee-founded urban populations of some parrot species (particularly *Amazona* spp.) often fare better than wild ones (Butler 2005). Although the nesting success of Florida Sandhill Cranes in modified habitats was once so low that these habitats were considered population sinks (Toland 1999), by now urban Florida Sandhill Cranes may outnumber nonurban ones (Nesbitt and Hatchitt 2008). One striking example is the Hawaiian Goose (*Branta sandvicensis*), which became extinct in the wild and was later reintroduced to the main Hawaiian Islands. On Hawaii (Big Island) and Maui, the birds mostly inhabit high-elevation shrublands and forest edges (their natural habitats) and their numbers remain low, but on Kauai they have colonized agricultural lands, golf courses, and other modified habitats and are now so numerous that hundreds are about to be transferred to other islands—a success called "a puzzling comeback" by one of the researchers (Hess 2011, BirdLife International 2012a). These examples show that the additional risks might be worth taking if populations in modified habitats considerably augment those living in relatively pristine ones, and particularly if modified habitats are the only ones available (as is the case for an increasing number of species worldwide).

The success of reintroductions in human-modified habitats can often be critically improved by public outreach programs (see, e.g., Simon et al. 2012, Ezaki et al. 2013, IUCN/SCC 2013, Harrell 2014). A massive outreach program was initiated in Louisiana after the first losses of reintroduced Whooping Cranes to illegal shooting, and it resulted in a rapid decrease in annual mortality due to such incidents, from $>30\%$ in 2011 to $<10\%$ from 2012 onward (Louisiana Department of Wildlife and Fisheries 2014, S. Zimorsky personal communication). A day might soon come when a typical species-reintroduction team will include experts on local culture and public relations. More generally, we have to realize that human-modified habitats are novel ecosystems that differ from old ones in complex ways. For example, predation pressure in human-modified habitats can be lower, as it is for Grasshopper Buzzards (*Butastur rufipennis*; Buij et al. 2013), or higher, as for many prey species of "suburban" predators such as large gulls (*Larus* spp.; Skórka et al. 2012). These differences demand increased flexibility from both the reintroduced animals and the people conducting the reintroductions; in some cases, such flexibility might be a beneficial result of interrupted cultural transmission.

ACKNOWLEDGMENTS

I thank G. Archibald, V. Flint, L. Fondow, V. Fridman, S.-R. Kang, S. King, T. Kitagawa, K. Mikhailov, M. Molukov, T. Perkins, W. Selman, E. and O. Smirensky, P. Tomkovich, and S. Zimorski for helpful discussions of the subject.

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