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Experimental identification of social learning in wild animals

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Field experiments can provide compelling demonstrations of social learning in wild populations. Social learning has been experimentally demonstrated in at least 23 field experiments, in 20 species, covering a range of contexts, such as foraging preferences and techniques, habitat choice, and predator avoidance. We review experimental approaches taken in the field and with wild animals brought into captivity and note how these approaches can be extended. Relocating individuals, introducing trained individual demonstrators or novel behaviors into a population, or providing demonstrator-manipulated artifacts can establish whether and how a particular act can be socially transmitted in the wild and can help elucidate the benefits of social learning. The type, strength, and consistency of presented social information can be varied, and the provision of conditions favoring the performance of an act can both establish individual discovery rates and help determine whether social information is needed for acquisition. By blocking particular avenues of social transmission or removing key individuals, routes of transmission in wild populations can be investigated. Manipulation of conditions proposed to favor social learning can test mathematical models of the evolution of social learning. We illustrate how field experiments are a viable, vital, and informative approach to the study of social learning.

Social learning is taxonomically widespread, with both invertebrates and vertebrates acquiring information from either the behavior of other individuals or the products of their behavior (Galef & Laland, 2005; Leadbeater & Chittka, 2007). Social learning has been demonstrated in multiple behavioral contexts of adaptive significance, such as the learning of foraging resources, foraging techniques, settlement locations, travel routes, predator responses, and mate preferences (Galef & Laland, 2005; Griffin, 2004; Leadbeater & Chittka, 2007). Moreover, social learning underlies the emergence and maintenance of cultures (Boyd & Richerson, 1985). Thus, the mechanisms underlying social learning, their evolution and development, and their adaptive consequences are all important topics relevant to a range of fields, including ethology, ecology, psychology, anthropology, and evolutionary biology. Here, we argue that field studies are a vital but underused part of answering questions about these topics. Field experiments complement and extend other approaches to the study of social learning and should not be isolated from them.

Multiple processes underlie social learning, and research into social learning is not characterized by a single question (Galef, 1988; Heyes, 1994). Consequently, any single approach will be inadequate to provide a complete explanation of the causes and consequences of socially learned behaviors. Observational and experimental studies in the laboratory and the wild, combined with theoretical and even archeological approaches, are all important and valuable methodologies (Dawkins, 2007; Franz & Nunn, 2009; Haslam et al., 2009; Kendal, Kendal, Hoppitt, & Laland, 2009; Lefebvre, 1995; Reader, 2004; van Schaik et al., 2003; Whiten et al., 1999; see also the contents of this special issue: Kendal, Galef, & van Schaik, 2010). Particularly valuable are cycles of feedback between experiments in captivity and those in the field, as is experimental study in the laboratory of behavior patterns observed in the wild and ascribed to social learning. We describe such examples below, alongside pure field experiments.

The value of field experiments. Use of manipulative experimental approaches with wild populations is relatively new in the field of social learning, possibly fueled by the recent explosion of interest in nonhuman animal cultures (Fragaszy & Perry, 2003; Heyes & Galef, 1996; Laland & Galef, 2009). As was pointed out most emphatically by Laland and colleagues (Laland & Hoppitt, 2003; Laland & Janik, 2006) but has been a point made repeatedly over the history of social-learning research (e.g., Galef, 1976), a lack of direct evidence for social learn-

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ing's maintaining community-specific traditions in the wild represents a significant stumbling block for research, particularly for assessment of the importance of social learning in natural circumstances. Population differences in behavioral repertoires have been ascribed to differential innovation being followed by social learning within a locality, with the *method of exclusion* used to rule out genetic or ecological explanations for population differences (e.g., van Schaik et al., 2003; Whiten et al., 1999). However, ruling out both ecological and genetic factors as alternative explanations is considered both highly problematic and logically insufficient by many commentators (Laland & Galef, 2009). Moreover, since social learning allows animals to acquire behavior appropriate to local conditions, perhaps the most important instances of social learning will be those linked to local ecology—the very examples ruled out by the method of exclusion. Controlled experimental manipulations, allowing convincing demonstrations of social influences on learning, are thus fundamental to confirming the existence of animal cultures and social learning, even when such experiments do not elucidate the precise social-learning mechanisms underlying animal traditions. Given the vast corpus of work examining social-learning processes in the laboratory that has provided a suite of useful approaches, field studies have much catching up to do. Yet their value is potentially immense.

Field experiments can demonstrate that social learning operates in free-living animal populations. Without such data, the most elegant laboratory demonstrations of social learning will fail to confirm that the same mechanisms are employed in the normal life of animals, thus leaving opaque the relevance and relation of the results of laboratory studies to ecology and to the evolution of social information use (Galef, 1976; Seppänen & Forsman, 2007). Unidentified features of field environments or field-rearing conditions may alter experimental outcomes (Cuthill, 1991). Social learning may be employed only in the idealized conditions of the laboratory, or, conversely, animals may be able to acquire behavior patterns individually in the laboratory but, in the wild, employ social learning for the same purpose. For example, alternative acquisition routes available in the wild may facilitate social learning, such as multiple demonstrators or demonstrators in long-lasting close proximity (e.g., mothers and infants).

Animals in the field have varied options available to them, whereas in the laboratory, the social and physical environment is typically more impoverished and options are more restricted. For example, foraging free-living animals could maintain established, rewarded behavior even when social information indicates that alternatives are available, whereas social learning might be the only route to food in a captive setting. Field studies also allow the diffusion (or lack thereof) of a behavior pattern to be monitored, and such diffusion may differ from expectations based on either payoffs resulting from engaging in a behavior pattern or patterns of diffusion observed in the laboratory (Kummer & Goodall, 1985; Laland & Hoppitt, 2003; Lefebvre & Palameta, 1988; Reader & Laland, 2003b). Possible causes of such differences in the patterns of diffusion observed in the laboratory and in nature could derive from the structure of social networks and patterns of interactions or from nondemonstrators influencing social learning. For example, bystanders may distract observers or disrupt demonstrators (Lefebvre & Giraldeau, 1994).

On a heuristic level, the constraints of field research can be useful in simplifying research questions and experimental designs to address core issues, and fieldwork can sharpen the relevance and methodology of laboratory experiments. Field experiments thus provide the opportunity to establish the mechanisms and benefits of social learning in wild populations, allowing researchers to go beyond the question "Is social information utilized?" and to examine a number of issues of applied and theoretical interest. Given the limitations of the field in the majority of study systems (including varied ethical and practical considerations; Cuthill, 1991), experiments that replicate the exacting control possible in the laboratory are difficult to devise. However, rigorous demonstrations of social learning, underlying processes, and adaptive consequences are feasible in the field. Below, we summarize approaches that have moved beyond observational data by employing some ingenious methods to demonstrate the occurrence of socially mediated learning among wild animals.

What are field experiments? We suspect that all readers will have an intuitive understanding of both *field* and *experiment*, but for clarity, we provide the operational definition that we used in our survey of the published social-learning literature: manipulations of free-living populations. These manipulations are typically transient or limited modifications of either well-defined habitat or individual characteristics. We do not include studies involving gross manipulations, such as cross-fostering members of one species to another, because in such cases the causal role of social information will be difficult to determine (Slagsvold & Wiebe, 2007). We exclude from our survey natural experiments, since manipulations are uncontrolled and are not performed by an experimenter, although we mention particular illustrative cases below.

Our delimitation between field and captive studies has arbitrary characteristics. For example, free-living animals may reside in areas impacted or provisioned by humans, resulting in effects on their behavior and evolution (McDougall, Réale, Sol, & Reader, 2006). Indeed, social learning may be a key part of allowing animals to cope with human impacts (Lee, 1991; Reader & Laland, 2003a; Whitehead, 2010). Moreover, field experiments may involve arbitrary or artificial stimuli or domesticated animal strains, whereas captive studies may use wild-caught animals or may closely recreate native environments. We strongly encourage captive studies using naturalistic environments, which provide many advantages over artificial captive environments. We exclude field experiments in which animals are not free-living at the time of testing, such as wild individuals placed in temporary enclosures in the field (e.g., the escape-route learning tests of Reader, Kendal, & Laland, 2003), even though such studies use individuals with natural experiences up to the point of testing. We suggest that our focus on free-living populations avoids an overly restrictive survey and captures the key feature that manipulations are conducted within a rich physical and social environment, with multiple options available to the animals.

Summary of aims. We have four aims: (1) to survey existing work; (2) to illustrate the advantages and disadvantages of current approaches; (3) to detail the essential requirements to confirm social learning; and (4) by including discussion of captive studies particularly relevant to fieldwork, to suggest additional or alternative approaches. On any criteria, demonstrations of social learning in wild populations are rare. We hope to encourage field research into a variety of questions concerning social learning.

Field Experiments

The survey. Our survey (Table 1) covers social learning in nonhuman animals, excluding examples of social information use where learning has not been definitively demonstrated. Thus, we exclude examples in which behavior has not been measured in the absence of either the producers of social information (henceforth, *demonstrators*) or their artifacts. For example, mate-choice copying (a form of social information use) was demonstrated in wild sailfin mollies (*Poecilia latipinna*), but the design did not incorporate a subsequent phase without demonstrators to test whether any learning had taken place (Witte & Ryan, 2002). Similarly, Hromada, Antczak, Valone, and Tryjanowski (2008) demonstrated that male red-backed shrikes (*Lanius collurio*) used the social information provided by food caches (impaled prey, artifacts of successful foraging) in making settlement decisions, but the authors did not observe behavior in the absence of the caches. We suspect that learning is likely in such cases, but it was not formally demonstrated.

We exclude cases of social information use without learning, not because we believe that it is unimportant or uninteresting, but because we believe that social learning is qualitatively different from social information use without learning. Although there are cases in which social information will be either long-lasting (e.g., animal products) or consistently available, learned behavior can be maintained after a social cue has been removed and behavior has been interrupted (Boyd & Richerson, 1985; Morand-Ferron, Doligez, Dall, & Reader, in press). For example, knowledgeable conspecifics mobbing a predator may be joined by a naive individual that continues mobbing when the conspecifics stop. However, if no learning has occurred, the naive individual will not respond to the predator if it reappears (Curio, Ulrich, & Vieth, 1978).

We roughly classify examples according to the nature of the principal manipulations performed: (1) manipulating physical aspects of the environment, (2) manipulating individual behavior (including manipulation of individual presence), (3) manipulating transmission routes, or (4) some combination of these. We also focus on the need for adequate control conditions to eliminate alternate explanations of social learning. We include in our survey social-learning field experiments producing negative results. The value of such experiments lies in demonstrating a lack of a need for social learning, particularly when purely observational data are suggestive of, and are readily interpreted as, illustrating behavioral traditions (Laland & Janik, 2006).

A recent review (Galef, 2004) highlighted field experiments as a promising approach to the study of traditional behaviors but listed only five such examples, three of which we would exclude from our survey (one was arguably nonmanipulative according to our definition,[1] another did not specifically test social learning,[2] and the third did not incorporate a control condition allowing comparisons of individual and social components of learning[3]). Our survey, unlikely to be exhaustive, expands considerably on this review but reveals that field experiments are still relatively rare. We document 23 studies, most published since Galef's (2004) review, covering 20 species, that demonstrate social learning in the field and 3 studies that provide no evidence for social learning. These important findings confirm that field experiments are viable and can inform us regarding social learning in natural contexts.

Manipulating the environment or populations wholesale: Coral reef fish translocation studies. In the most dramatic manipulations of the environment, the ground is figuratively pulled from under a population's feet, since its members are moved from their original range into a novel setting. If behavior patterns are maintained by social learning, rather than being channeled by some ecological constraint, moving an entire population into a new environment allows three predictions. First, if social learning is involved, the translocated population should, so far as possible, maintain its established traditions. Second, if the new location was previously home to another, now absent, population, the new arrivals will not necessarily adopt the traditions of the individuals that previously lived there. Third, if the new locale contains suitable demonstrators (e.g., members of the local population who exhibit a putative tradition), translocated individuals may acquire any putatively traditional behaviors that these local "demonstrators" exhibit. All three of these predictions hold true in the case of spatial behavior in coral reef fish.

Helfman and Schultz (1984) demonstrated that the third of these principles operates in free-living French grunts (*Haemulon flavolineatum*). Individual fish experimentally displaced to novel locations followed the native population on their daily travel routes toward shoaling sites and subsequently adopted these routes themselves when traveling alone, thus demonstrating social learning, in addition to social information use when demonstrators were present. Importantly, control fish, translocated to the same location after the native population had been removed and, thus, lacking opportunities to follow demonstrators, did not adopt the routes previously used by the removed individuals. These experimental data imply that daily shoaling sites were maintained via socially transmitted information between knowledgeable demonstrators

Table 1
Studies Applying a Field Experimental Approach to Social Learning in Nonhuman Animals (Ordered Chronologically)

Study	Species	Location	Approach	Behavior Pattern	Control Condition(s)	Outcome/Conclusion	Notes
Gould (1974, 1975a, 1975b)	Honeybee (*Apis mellifera*)	Open fields, Millbrook, New York	Trained demonstrators	Location of scented feeders	Variation of demonstrator waggle dance patterns by light manipulation	Social learning: Direction and distance of targets obtained from demonstrator within hive	To eliminate demonstrator cues on feeders, ocelli of demonstrators were covered, causing them to indicate a location they had not visited.
Jenkins (1978)	Saddleback (*Philesturnus carunculatus*)	Cuvier Island, New Zealand	Translocation to uninhabited island	Song dialects	Comparison with origin population	Social learning: Inferred by maintenance of song patterns from origin population; formation of long-lasting discrete song groups, each founded by 1–2 introduced birds; new recruits adopting these song groups; spread of new variants	At least five of the nine documented song patterns occurred within origin population. Sons sang songs of neighbors, not fathers, ruling out genetic inheritance from father.
Conover & Perito (1981)	Starling (*Sturnus vulgaris*)	Dairy farms, Connecticut	Starling tethered to predator model	Avoidance of predator (owl) model	Presentation of tethered conspecific only, of owl model and dead conspecific, of owl model and distress calls, repeated presentations of owl model	Social learning: Observers showed increased avoidance of owl model after pairing with tethered conspecific.	Birds learned to avoid model rather than site. Distress calls alone resulted in avoidance of model but no evidence of learning.
Helfman & Schultz (1984)	French grunt (*Haemulon flavolineatum*)	Tague Bay, U.S. Virgin Islands	Translocation of individuals to site with resident demonstrators	Schooling sites and travel routes	Translocated individuals with no resident demonstrators	Social learning: Translocated individuals adopted schooling sites and routes of residents.	Most controls were disoriented, but some may have attempted to maintain natal population's routes.
Lefebvre (1986)	Pigeon (*Columba livia*)	Urban Montreal, Canada	Trained demonstrators	Foraging task (box opening)	Separate population with no trained demonstrators; laboratory flock with demonstrator	Social learning: Behavior spread faster in experimental than in control population.	Box-opening spread faster in wild than in laboratory population, probably due to turnover of birds in open population.
Warner (1988, 1990b)	Bluehead wrasse (*Thalassoma bifasciatum*)	Coral reef, San Blas Islands, Panama	Translocation of populations	Mating site choice	Population removal and replacement in same location	Social learning: Inferred by loss of mating sites in translocated populations	Translocated fish adopted novel mating sites, subsequently maintained over several generations.
Warner (1990a)	Bluehead wrasse (*Thalassoma bifasciatum*)	Coral reef, San Blas Islands, Panama	Translocation of all males or all females within a population	Mating site choice	Population removal and replacement in same location	Social learning: Mating site preferences lost when females moved; hence, maintained via female activity	Smaller females were known to regularly accompany large ones during travel, which may provide a mechanism for transmission of site preferences.
Michelsen, Andersen, Storm, Kirchner, & Lindaner (1992)	Honeybee (*Apis mellifera*)	Würzburg, Germany	Mechanical demonstrator	Location of scented targets	Motionless mechanical demonstrator; variation of waggle dance patterns	Social learning: Distance and direction of targets obtained from demonstrator	Demonstrator in hive; thus, flight patterns outside hive a result of learning from demonstrator.
Langen (1996)	White-throated magpie jay (*Calocitta formosa*)	Santa Rosa National Park, Costa Rica	Trained demonstrator	Foraging task (box opening)	No demonstrator or nonperforming demonstrator	Social learning: Observers later opened box in the absence of the demonstrator (T. A. Langen, personal communication, 04/20/2010).	Performance in absence of demonstrators not quantified.

Table 1 (Continued)

Study	Species	Location	Approach	Behavior Pattern	Control Condition(s)	Outcome/Conclusion	Notes
Banks & Guilford (2000)	Homing pigeon (*Columba livia*)	Oxfordshire, U.K.	Trained demonstrator	Homing performance	Naive demonstrator	No social learning: No improvement in solo homing performance following demonstration	Only one demonstration was provided to each observer.
Fritz, Bisenberger, & Kotrschal (2000)	Greylag goose (*Anser anser*)	Grünau, Austria	Human demonstrator	Foraging task (box opening)	Training with already opened box	Social learning: Birds shown box opening all learned technique; controls did not.	Human-imprinted goslings; free-living but provisioned.
Midford, Hailman, & Woolfenden (2000)	Florida scrub jay (*Aphelocoma coerulescens*)	Archbold Biological Station, Florida	Trained demonstrators within family groups	Digging for peanuts in center of marked patch	Sham-trained demonstrator families	Social learning: Juveniles in trained families foraged in patch even when alone.	Blocking scrounging reduced social information use.
Esch, Zhang, Srinivasan, & Tautz (2001)	Honeybee (*Apis mellifera*)	Farmland, Würzburg, Germany	Trained demonstrators	Recruitment to feeders	Disoriented demonstrators via manipulation of optic flow	Social learning: Hive mates visited feeder at distance indicated by demonstrator dance.	Demonstrators were never at feeder that hive mates visited; Dance was elongated by optical flow manipulation.
Sherman & Visscher (2002)	Honeybee (*Apis florea*)	California	Trained demonstrators	Recruitment to food sources	Disoriented demonstrators via manipulation of light	Social learning: Colonies with undisturbed waggle dancers recruited to demonstrators' feeders.	Disruption to social information reduced effective nectar collection (under certain conditions).
Reader, Kendal, & Laland (2003)	Guppy (*Poecilia reticulata*)	Freshwater streams, Trinidad	Demonstrators created by placing shoal at one patch	Foraging patch choice	Counterbalanced	Social learning: Observers returned to demonstrated patch after removal of demonstrators.	Artificial feeders utilized.
Gajdon, Fijn, & Huber (2004)	Kea (*Nestor notabilis*)	Semiurban New Zealand	Trained demonstrator	Foraging task (tube lifting)	Baseline predemonstration trials	No social learning: Behavior did not spread to observers.	Trained demonstrator's access to apparatus limited by dominant solver of task.
Farina, Grüter, & Díaz (2005)	Honeybee (*Apis mellifera*)	Buenos Aires, Argentina	Demonstrators created by feeding scented solution outside hive	Floral odor learning	Control hive with no scented solution	Social learning: Food transfer within hive promotes learning of odor by recipient.	Social learning reflected in both spontaneous response and learning a conditioned response to odor.
Nocera, Forbes, & Giraldeau (2006)	Bobolink (*Dolichonyx oryzivorus*)	Nova Scotia, Canada	Decoys and song playback	Habitat selection	No decoys or playback	Social learning: Birds preferentially settled on sites with social cues.	Effect most pronounced in young males; settlement decisions measured 1 year after social cues removed.
Nocera et al. (2006)	Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*)	Nova Scotia, Canada	Decoys and song playback	Habitat selection	No decoys or playback	No social learning: Social cues had no effect on settlement.	Settlement decisions measured 1 year after social cues removed.
Thornton & McAuliffe (2006)	Meerkat (*Suricata suricatta*)	South African Kalahari	Provisioning of live prey by experimenters, replicating helper behavior	Scorpion handling	Provisioning of dead prey or other food (egg)	Social learning: Superior handling after experience with live prey	Helpers provision juveniles with live prey they would otherwise rarely encounter.

Table 1 (Continued)

Study	Species	Location	Approach	Behavior Pattern	Control Condition(s)	Outcome/Conclusion	Notes
Seppänen & Forsman (2007)	Collared flycatcher (*Ficedula albicollis*)	Gotland, Sweden	Manipulated apparent demonstrator behavior	Nest site choice	Counterbalanced	Social learning: Flycatchers copied tits' apparent nest site choices.	Copying rates increased with arrival date. Demonstrators were resident great tits *Parus major* and blue tits *P. caeruleus*.
Seppänen & Forsman (2007)	Pied flycatcher (*Ficedula hypoleuca*)	Oulu, Finland	Manipulated apparent demonstrator behavior	Nest site choice	Counterbalanced	Social learning: Flycatchers copied tits' apparent nest site choices.	Copying rates increased with arrival date. Demonstrators were resident great and blue tits.
Betts, Hadley, Rodenhouse, & Nocera (2008)	Black-throated blue warbler (*Dendroica caerulescens*)	New Hampshire	Male decoy and song playback	Habitat selection	No decoys or playback	Social learning: Birds preferentially settled on sites with social cues.	Settlement decisions measured 1 year after social cues removed; young males more likely than older birds to settle on low-quality sites with social cues.
Betts et al. (2008), Treatment 2	Black-throated blue warbler (*Dendroica caerulescens*)	New Hampshire	Decoys and playback of fledgling begging, female calls, and male song	Habitat selection	No decoys or playback	Social learning: Birds preferentially settled on sites with social cues.	Settlement decisions measured 1 year after social cues removed; young males more likely than older birds to settle on low-quality sites with social cues.
Thornton (2008)	Meerkat (*Suricata suricatta*)	South African Kalahari	Food presented with experienced demonstrator	Novel food consumption	Presentation of food in absence of demonstrator	Social learning: Pups with demonstrators were more likely to accept novel food when later tested alone.	Demonstrators occasionally spontaneously fed observers the novel foods presented.
Davies & Welbergen (2009)	Reed warbler (*Acrocephalus scirpaceus*)	Wicken Fen, Cambridgeshire, U.K.	Demonstrator behavior induced by playbacks	Mobbing of brood parasite (cuckoo model)	Baseline predemonstration trials, presentation of harmless intruder (parrot model)	Social learning: Birds increased mobbing of cuckoo model after observation of neighbors' response.	Demonstrators' mobbing of control (parrot) model did not subsequently increase mobbing in observers.
Thornton & Malapert (2009)	Meerkat (*Suricata suricatta*)	South African Kalahari	Trained demonstrator	Food landmarks	Groups without demonstrators	Social learning: Observers developed preference to feed at demonstrated landmark.	Subsequent individual learning quickly broke down group traditions.
Müller & Cant (in press)	Banded mongoose (*Mungos mungo*)	Queen Elizabeth National Park, Uganda	Used natural variation in demonstrator behavior	Foraging task with two solutions (open by smash or bite)	Counterbalanced demonstrated solution; presented opened tasks, no task, or demonstrator not interacting with task	Social learning: Pups used demonstrated opening technique 2–4 and 4–10 months after demonstration.	Adult demonstrators. Social learning did not result in increased behavioral homogeneity in population.
van de Waal, Renevey, Favre, & Bshary (2010)	Vervet monkey (*Chlorocebus aethiops*)	Loskop Dam Nature Reserve, South Africa	Manipulated apparent demonstrator behavior	Foraging task with two solutions (box opening)	Counterbalanced demonstrated solution across groups	Social learning: Observers manipulated same side of box as female, but not male, demonstrator	Demonstrator could be present during test, but satiated and thus not interacting with task (E. van de Waal, personal communication, 03/23/2010).
Reader (unpublished data)	Carib grackle (*Quiscalus lugubris*)	Urban parkland, Barbados	Trained demonstrators	Foraging task (box opening)	Group and individuals without demonstrators in field and captivity	Social learning: Birds began box opening after interaction with demonstrators.	Demonstrators released back into local population. Relatively few birds acquired box opening.

Note—The survey is not exhaustive. In particular, we do not fully survey birdsong work or the many honeybee foraging experiments but, instead, indicate key, early, or definitive studies. The term *demonstrator* refers to the individual learned from, regardless of whether they were trained by the experimenters.

and initially naive young observers, who, in turn, would subsequently become demonstrators for other new recruits to the population.

In a more elaborate manipulation, Warner (1988) replaced entire populations of bluehead wrasse (*Thalassoma bifasciatum*) in Panama with populations captured on other reefs. The introduced fish discovered and adopted novel mating sites to which they remained faithful for 12 years (four generations). These sites were novel in that they had not been used by the population that had lived there before them. Follow-up studies transplanted the male and female portions of a population separately (Warner, 1990a). Removal of females, but not of males, from a population resulted in the loss of mating sites. Thus, female behavior was responsible for the maintenance of the mating site traditions, a view supported by observations that females arrive together at mating sites.

Warner (1990b) also performed whole-population transplants twice in succession. Mating sites changed after the first transplant. However, and consistent with the hypothesis that transplanted individuals make similar choices about where to mate, sites used after the second transplant were very similar to those used after the first. Warner (1990b) suggested that resource assessment can lead to a predictable pattern of mating site use but that this resource assessment does not occur when a tradition is already in force, which is particularly likely when quality differences between resources are relatively small and costly to assess. In the case of the mating sites, it seems that a surplus of sites is available, and it is more important to be where other individuals are mating than at a slightly superior site where others are not mating. As Warner (1990b) pointed out, when social learning is operating, it may be impossible to predict behavior without knowledge of the prior history of the population. Such experiments, which elegantly demonstrate that local ecology is not fully responsible for gross interpopulation differences in behavior, provide convincing arguments that social learning, rather than environmental constraints, underlie animal traditions that persist over multiple generations.

“Natural” translocations: Interpopulation migrations. The wholesale manipulations of populations (or, effectively, of the environment that they live in), described above in fish, would be problematic for many species and sites, although human introductions of species are numerous for both mammals and birds (Sol, Bacher, Reader, & Lefebvre, 2008; Sol, Lefebvre, & Timmermans, 2002) and may provide useful opportunities for social-learning studies (e.g., Jenkins, 1978). Emigrations and immigrations between neighboring populations may also provide parallel data, in the form of natural experiments. However, this approach may be compromised if the behavioral repertoires of the source and destination population are not well known. This is frequently the case because extended research is required to uncover behavioral repertoires and, thus, researchers tend to focus on a particular population. For example, observation of primate groups requires lengthy habituation periods, compromising the following of emigrants from study groups. Moreover, natural experiments are likely to lack the control data needed to firmly establish social learning.

One interesting case study concerns the *grooming handclasp*, a putative social custom among the chimpanzees (*Pan troglodytes*) of Mahale, Tanzania (among others) that differs in the details of its performance between different communities (Nakamura & Uehara, 2004). At Mahale, a female (Gwakulo) changed the way she performed the grooming handclasp after moving between two adjacent communities. After she moved, she adopted the style common in her new community, and individuals in her new group began to perform the style originally preferred by Gwakulo, although only in interactions with her. The grooming handclasp is a product of two interacting individuals, so it remains unknown whether Gwakulo learned the alternative technique after arrival or whether any members of her new group learned the imported technique from her. If future studies document more such examples of intergroup migration followed by changes in behavior of individuals within the recipient group, the case for regional diffusions based on geographic distance (e.g., van Schaik et al., 2003) will be considerably strengthened.

Manipulating the environment: Novel resources or tasks. Less extreme than replacement of the entire habitat for a group of individuals, other forms of manipulating the environment have involved the provision of various resources that are otherwise unavailable. Such provisioning has involved both entirely novel resources and those that conspecifics are utilizing in other locales (Reader, Nover, & Lefebvre, 2002). The goal of provisioning is to discover whether a behavior is locale specific because of local knowledge or because of differences in local resources. Novel responses to the new resources and any subsequent diffusion of these novel responses through a group can be examined, with particular reference to whether diffusion occurs through individual or social learning.

Matsuzawa and colleagues (Biro et al., 2003; Matsuzawa, 1994; Matsuzawa & Yamakoshi, 1996) adopted this approach, providing a naturally nut-cracking community of wild chimpanzees at Bossou, Guinea with two species of nuts unavailable at Bossou: the *Coula* nut, cracked by chimpanzees elsewhere in West Africa, and the *Panda* nut, cracked by chimpanzees living just 50 km from Bossou.

Initially, a single individual was observed at Bossou cracking the *Coula* nuts without hesitation, with other group members showing intense interest in her nut-cracking and the majority of the group gradually adopting *Coula* nut cracking. *Panda* nuts, on the other hand, were cracked only a handful of times, then completely ignored by all. These observations could be explained by the initial *Coula* cracker’s being a past immigrant to Bossou, from a community where *Coula* cracking was habitual, and her behavior’s influencing the rest of the group to accept *Coula* nuts. The introduced nuts did not require innovation in tool-using techniques, only adaptation of an existing technique to an unfamiliar target item. Although recent genetic data suggests that the initial *Coula* nut cracker was indeed an immigrant (Shimada et al., 2004), the role of this probably knowledgeable individual in diffusion of the behavior through the Bossou community of chimps remains questionable. Specifically, there is little to suggest that social, rather than individual, learning was responsible for an increasingly large proportion of the Bossou group adapting their existing nut-cracking skills to the processing of a previously unfamiliar nut. That said, the edible *Panda* nut did not become a similarly attractive item for the chimpanzees. In a sense, the community thus acted as its own control group, providing circumstantial evidence for the influence of a knowledgeable demonstrator in facilitating novel behavior in its observers. However, although the presentation of novel resources or tasks can determine the readiness of a population to utilize them and potentially can exclude social learning as an explanation, proof of social learning is not possible with such a manipulation (but see Kendal, Custance, et al., 2010).

Recently, Gruber, Muller, Strimling, Wrangham, and Zuberbühler (2009) tackled the problems associated with studying a single population, and the difficulty of drawing inferences from a single introduction event with no clear control or comparison, by performing identical manipulations with two communities of chimpanzees living under highly similar ecological conditions but with considerably divergent tool use repertoires (the Sonso and Kanyawara communities of Budongo Forest and Kibale National Park, Uganda). At both sites, Gruber et al. drilled and baited holes in logs with honey, first at depths that chimpanzees could access by hand, then deeper, so that the honey could no longer be reached without a tool. Kanyawara chimpanzees, whose tool repertoire includes use of sticks in extractive foraging, spontaneously used sticks to obtain honey from the deeper hole. Sonso chimpanzees, never observed using sticks for foraging, instead manufactured leaf sponges for the task. Leaf sponging is a "chimpanzee universal" (Whiten et al., 2001): a tool use behavior observed at all chimpanzee field sites (including Kanyawara) so far studied.

This segregation of responses was absolute; not a single Sonso chimpanzee used a stick tool, and not a single Kanyawara chimpanzee used a leaf sponge. The conclusion that the behavior of both communities was scaffolded by their existing knowledge of tools is compelling, although a direct demonstration of social learning being responsible for either (1) maintaining the divergence between the existing tool use repertoires of the two communities or (2) conformity in both communities' responses to the experimental apparatus is lacking (Call & Tennie, 2009). Nonetheless, Gruber et al.'s (2009) work provides a fascinating glimpse into the possibility that situations involving multiple populations and echoing the highly controlled captive systems examined by Whiten and his colleagues (Whiten, Horner, & de Waal, 2005; Whiten et al., 2007) can be constructed and examined in the wild.

Manipulating individual behavior: Foraging in fish and mammals. Several field studies, by manipulating the social environment, have focused on the role of key individuals in effecting changes in the behavior of others within their group. Experimental manipulations typically entailed altering the behavior of key individuals from its current state either (1) by explicit training or exposure to specific stimuli or (2) through direct control by experimenters causing key individuals to provide pertinent information to other group members.

The latter design is exemplified by work on Trinidadian guppies (*Poecilia reticulata*) and vervet monkeys (*Chlorocebus aethiops*). Reader et al. (2003) examined foraging site choice by guppies in the wild by creating two visually distinct feeding sites of equal quality. One of the sites also contained a small shoal of locally captured fish held within a transparent container, effectively creating a group of demonstrators feeding at one site. Fish preferentially entered the feeding site with the shoal, and, crucially, this preference was maintained in a subsequent test phase, when the demonstrator shoal was no longer present, demonstrating social learning of a feeding site as a result of a tendency to approach feeding conspecifics.

Van de Waal, Renevey, Favre, and Bshary (2010) examined foraging in free-living vervet monkeys, elegantly taking advantage of the fact that dominant individuals monopolized a feeding task to create a single demonstrator in each group without the need for training in isolation. By providing dominant individuals with a feeding task with two solutions (two doors to open a box), but with one solution blocked, observers in different groups viewed only one of the two solutions. Observers were then tested with both solutions available, with observers of female, but not male, demonstrators preferentially exhibiting the demonstrated solution.

In a compelling series of studies, Thornton and colleagues examined the role of social learning in the development of wild meerkats' foraging behavior (Thornton, 2008; Thornton & McAuliffe, 2006; Thornton & Raihani, 2010). Initial work focused on helpers (individuals older than 3 months who assist parents in rearing young) teaching prey-handling skills to pups through the provisioning of pups with potentially dangerous but disabled scorpions either with their stings removed or already killed (Thornton & McAuliffe, 2006). In playback experiments in which the begging calls of pups either younger or older than those present were broadcast from hidden speakers, helpers provided a higher proportion of dead or disabled prey in response to younger pup calls and more intact prey to older pup calls, thus showing sensitivity to the age of the perceived audience (Thornton & McAuliffe, 2006). Pups given experience of disabled live prey derived the largest benefits in future prey-handling attempts, confirming the benefits of this provisioning.

Meerkat pups were also tested for their acceptance of novel foods by virtue of their association with demonstrators (Thornton, 2008). Pups received unfamiliar food (eggs) with or without an accompanying helper. About half the pups tasted the eggs when a helper was nearby and itself feeding on the food, whereas none did so when alone, and in a subsequent test, in which the same pups were presented with eggs and no helper, only those pups that had previously eaten eggs did so. Pups given two consecutive trials with only eggs and no helper did not start feeding on eggs until they were introduced to them by a helper. Taken together, these findings suggest that the experience of feeding on an unfamiliar food together with a knowledgeable conspecific demonstrator significantly sped up pups' acceptance of that food. Similar results were obtained in another set of tests involving scorpions (Thornton, 2008). Data from the mongoose (*Mungos mungo*) extend on these findings, showing that foraging techniques, as well as food preferences, can be socially acquired and long-lasting (Müller & Cant, in press). Adults presented with plastic containers filled with food were found to consistently open them one of two ways, by smashing or biting. Later, when dependent pups were present, demonstrators were given containers to open. Pups exhibited the same opening technique as their demonstrator when independent and away from the adult demonstrator, even 10 months later. Control conditions, in which demonstrators either received ready-opened containers or no containers, did not result in pups' matching the preferred technique of the demonstrator, thus eliminating the possibility that matching behavior between pups and demonstrators resulted from a tendency for individuals with similar preferred techniques to associate together. Such research is particularly compelling because it mirrors the likely daily experiences of meerkat and mongoose pups and, as such, can inform us of the importance of social learning in the development of young individuals' foraging skills (see also Lonsdorf & Bonnie, 2010).

Manipulating individual behavior: Habitat selection and mobbing responses in birds. Birds of many species prospect for nesting sites (Doligez, Danchin, & Clobert, 2002). In a simple and elegant experimental manipulation, Seppänen and Forsman (2007) manipulated the apparent nest site choices of resident great and blue tits before the arrival of two species of migratory flycatchers by painting circles on the front of tit nestboxes and triangles on nearby empty nestboxes (or vice versa). As a result, it appeared that all the tits in each study location had chosen to nest in boxes with one of the two arbitrary symbols. Empty nest boxes painted with the same symbols were made available for flycatchers. The late-arriving migrants copied the apparent nest site choices of the resident tits, demonstrating social learning from heterospecifics. Individuals differed in their utilization of the available social information; in this case, late arrivals were more likely than early arrivals to use social information from resident birds. It is not known whether nest site choices in subsequent years were also affected by the manipulation of social information.

Nocera, Forbes, and Giraldeau (2006) addressed social information use in habitat selection by two synchronously breeding bird species. They provided social cues of habitat choice in the form of conspecific decoys and song playback after the breeding season in one year and then measured visits to the study plots in the subsequent year in the absence of social cues. Social learning could thus be assessed. One species, the bobolink (*Dolichonyx oryzivorus*), demonstrated social learning even to suboptimal habitats, and another, less social species, Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*), did not. A related study of black-throated blue warblers (*Dendroica caerulescens*, a migrant songbird) addressed the relative role of habitat quality and social information in habitat choice by providing social information in habitats of varied quality (Betts, Hadley, Rodenhouse, & Nocera, 2008). The effect of social information (decoys and playbacks) was compared with a control condition (silence), with the social information presented one year and settlement decisions assessed the next. Young birds were more likely than older birds to immigrate to low-quality sites because of social information. Again, as in bluehead mating site choice (Warner, 1990b), social information can override the available "ecological" information, at least for a subset of the population. An observational study of the warblers showed that male song in the postbreeding season was a reliable correlate of breeding success, and thus social cues provided a useful index for habitat quality (Betts et al., 2008). This finding raises the possibility that particular transmission avenues can be deliberately blocked by experimenters to investigate social learning. Moreover, anthropogenic noise (Slabbekoorn & Ripmeester, 2008) may block such social information, illustrating how anthropogenic disturbance could disrupt social learning.

Another compelling playback study manipulated demonstrator behavior by the playback of mobbing calls, investigating how birds respond to potential brood parasites (Davies & Welbergen, 2009). Mobbing call playback caused reed warblers (*Acrocephalus scirpaceus*) to mob cuckoo or parrot models presented to them, while their nesting neighbors could observe. Subsequent tests of model presentations to the neighboring birds found that mobbing responses to the cuckoo, a harmful brood parasite at the study site, were acquired and maintained even 6 days later, whereas mobbing of parrots, not a brood parasite, was not acquired by the neighbors. The finding of differential learned responses to potentially harmful and harmless models is strikingly similar to the findings of studies of the role of predispositions in predator avoidance learning in captive macaques, where avoidance of snakes, but not flowers, is socially transmitted (Mineka & Cook, 1988). Reed warblers may preferentially learn about cuckoos because of a genetic predisposition or because of previous exposure to cuckoos at the field site (Davies & Welbergen, 2009). The experiment thus illustrates the important message that social learning, ecology, and genetic predispositions will interact in the formation and fine-tuning of behavioral responses. Social learning cannot be viewed as a stand-alone method of acquiring behavior that is independent from either genes or environment.

Manipulating individual behavior: Training demonstrators. Perhaps the most prolific of our three subcategories of field experiments incorporates studies that undertake a combination of manipulations of both the environment and individual behavior. Such approaches provide particularly powerful tests of social learning. Manipulating the environment exposes individuals to problems to be solved (often involving novel tasks or apparatuses, thus increasing the likelihood that the solution needs to be learned), whereas manipulating individuals introduces a salient and specific behavior whose subsequent appearance in others (when demonstrators are removed) can provide compelling evidence for the spread of information by social learning, particularly if compared with the behavior of control groups without demonstrators.

In what is, to our knowledge, the earliest such design, Lefebvre (1986) studied the establishment of a foraging tradition in feral pigeons by training demonstrators in captivity and then releasing them into a group of naive conspecifics. The task, piercing the covers of grain boxes, was acquired more rapidly by members of the group with demonstrators than by members of a control group without demonstrators. The control group did discover box piercing for themselves, but with much greater latency than the group with trained demonstrators, and only following accidental tearing of box covers by birds walking on them when they were rain-soaked (Lefebvre & Palameta, 1988). Interestingly, a captive group tested on an identical design with a single trained demonstrator experienced delayed diffusion of the behavior, probably because of scrounging by naive individuals. Removal of knowledgeable individuals from the captive group, simulating the emigration of individuals that would occur in open populations, sped the spread of box piercing. A similar test presented to a feral vervet monkey troop in Barbados provided no evidence for social learning. One juvenile male discovered how to open the boxes and subsequently opened boxes while in close proximity to other troop members on over 70 occasions. However, the behavior never spread (Lefebvre & Palameta, 1988).

Training of demonstrators on a foraging task has also provided evidence of social learning in white-throated magpie jays (*Calocitta formosa*) and Florida scrub jays (*Aphelocoma coerulescens*) (Langen, 1996; Midford, Hailman, & Woolfenden, 2000). Midford et al. trained and tested birds in family groups. The task involved digging for peanuts hidden inside conspicuously marked rings, and training continued until at least one member of the group became proficient. In subsequent seasons, the trained individuals were repeatedly given the opportunity to demonstrate their knowledge in front of newly fledged young. Control family groups that contained no trained individuals had no young acquire the task, whereas juveniles hatched into trained families acquired the behavior from older members of their group and, crucially, performed it not just in their presence (social information use), but also at feeding sites before demonstrators arrived (learning), although unfortunately, the article does not indicate how often juvenile performance was observed before demonstrator arrival. Interestingly, in contrast with findings from pigeons (Giraldeau & Lefebvre, 1987), the opportunity for juvenile jays to scrounge during demonstrations, increased experimentally by dividing food items into several pieces, appeared to enhance rather than inhibit learning. Furthermore, the social status of the trained individual appeared to affect opportunities to demonstrate; the presence of naive dominants inhibited subordinate models from performing, indicating that the identity of an innovator can have important consequences for the fate of innovations.

Using two artificially created landmarks and trained demonstrators exhibiting a preference for one over the other, Thornton and Malapert (2009) examined the transmission of foraging patch preferences in wild meerkats. Individual demonstrators were trained to associate food rewards with one of two locations marked by distinctive landmarks, and they had subsequent opportunities to perform their choices in front of, and be joined at the landmarks by, naive members of their group. Although untrained individuals initially showed no preferences for one landmark over the other, through repeated demonstrations by both trained conspecifics and, later, untrained individuals who had developed a preference by virtue of having been rewarded in the presence of trained models, a simple tradition of choosing the demonstrated landmark developed in several replicate groups. In two control groups without any trained demonstrators, no such traditions emerged. Interestingly, however, the traditions were relatively short-lived, with preferences for the two landmarks becoming equal within days, probably a result of individual learning about the alternative landmark. The Thornton and Malapert study provides a rare glimpse into both the appearance and the gradual breakdown of group traditions and confirms individual learning as a powerful modifier of socially acquired behavior.

Gajdon, Fijn, and Huber (2004) combined the training of demonstrators in a wild population of keas (*Nestor notabilis*), a highly social species established to be a proficient social learner in the laboratory (Huber, Rechberger, & Taborsky, 2001), with presentation of a novel experimental apparatus. Rather than choosing between alternatives, individual keas needed to learn to solve a novel foraging task. A single individual from a wild population was trained out of sight of other birds and was then allowed to perform in view of naive observers. Surprisingly, the trained model did not appear to aid naive observers' learning of the task. Only 3 of 21 naive birds learned to solve the task, and access to demonstrators failed to effect any increase in the frequency with which other birds interacted with the apparatus. The contrast with captive studies of keas, including a pilot experiment with an apparatus identical to that used in the wild, is stark. The performance of trained demonstrators outside of a laboratory setting is often hard to control, a problem encountered repeatedly in work bridging the gap between experiments with captive and wild animals (e.g., Drea & Wallen, 1999; Langen, 1996; Nicol & Pope, 1994). In the Gajdon et al. study, the trained kea demonstrator and most naive keas were prevented from interacting with the apparatus by a dominant individual who had learned (possibly by having observed the demonstrator) to solve the task. Such problems could be solved by designing the apparatus so that the demonstrator can manipulate it without disturbance—for example, by either allowing only the demonstrator access to the apparatus or placing the demonstrator within a transparent enclosure—although such methods carry the disadvantage that demonstrators and observers cannot interact together with the apparatus. Such a methodology has been used by one of the authors (S.M.R.) to move captive-trained birds from site to site and to provide multiple demonstrations at each field site by sequentially revealing tasks for the demonstrator.

Although foraging-related tasks constitute the most common forms of demonstrator training in studies of social learning, training demonstrators in other domains provides interesting parallel designs with similar ecological relevance. For example, Banks and Guilford (2000) trained homing pigeons to navigate back to their home loft through repeated releases from a distant site. Following training, during which the birds gradually improved in their ability to home, each demonstrator was released with a single naive conspecific and was allowed to demonstrate the homing route once. During paired flight with a knowledgeable partner, the performance of inexperienced birds exceeded that of fully naive control pairs (confirming that they were, indeed, receiving an accurate demonstration of the homing route). However, on a subsequent solo release, the tutored birds homed no faster than control birds, indicating that experiencing the performance of a knowledgeable navigator does not aid navigational learning, possibly due to a form of overshadowing between social and navigational cues, producing a scrounging-like *passenger/driver* effect (Burt de Perera & Guilford, 1999). Nonetheless, it is possible that repeated demonstrations or larger demonstrator groups would enhance the social learning of travel routes. The Banks and Guilford study has obvious relevance to any species whose members travel in groups and is particularly innovative, since animal movement patterns present many fascinating questions regarding potential traditions. For example, little is currently known about the precise role of social (and individual) learning, relative to genetically encoded direction preferences (Helbig, 1991; Mukhin, Kosarev, & Ktitorov, 2005; Plotkin, Byles, Rostal, & Owens, 1995) in the establishment, maintenance, and fine-tuning of migration routes in annual long-distance migrants that travel in mixed-age, mixed-sex, and mixed-experience groups. The fact that novel migration routes can evolve rapidly (Berthold, Helbig, Mohr, & Querner, 1992) reinforces the message that genetic adaptations may evolve quickly and should not be excluded as an explanation for the appearance of novel behavior patterns.

Finally, in populations in which the temporary isolation, training, and reintroduction of designated models into a group of naive conspecifics is not feasible, fortuitous events can simulate the appearance of trained demonstrators. Hannah and McGrew (1987) studied semicaptive chimpanzees in Liberia, who were released, one by one, from a sanctuary into an increasingly self-sufficient (although still provisioned) existence on a 10-ha island. Within hours of release, Samantha, the 11th individual released, was cracking oil-palm nuts with a stone hammer, a behavior never previously observed in any of the other individuals. Within a month, 9 of the 13 other individuals released on the island were also cracking nuts, some with the aid of materials introduced onto the island by researchers following the initial observations of nut cracking. Although there was no equivalent, matched group without a potential demonstrator, the evidence is suggestive of a key role for a single demonstrator in the diffusion of the behavior. However, the speed with which nut cracking spread through the population contrasts with the lengthy developmental time course of chimpanzees' tool-using skills in general (Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, Eberly, & Pusey, 2004; see Lonsdorf & Bonnie, 2010). Nut-cracking individuals thus may not have acquired nut cracking from Samantha. Hannah and McGrew speculated that, instead, they may already have known how to nut crack and simply had "their memories prompted by her actions" (p. 43).

Honeybee social learning of food locations and odors. Honeybees socially learn from conspecifics within the hive. We cannot fully review the many published studies here or in Table 1 but do point to experiments that illustrate a variety of valuable approaches to field social-learning experiments. For example, demonstrators can be created by feeding them scented foods (Farina, Grüter, & Díaz, 2005) or training them to particular locations (Gould, 1975b). Social cues such as the waggle dance can be modified or eliminated in many ways—for example, by manipulations of the optical or light environment (Esch, Zhang, Srinivasan, & Tautz, 2001; Sherman & Visscher, 2002). Moreover, data on the dance of honeybees have led to the construction of an effective mechanical demonstrator that can be precisely controlled by experimenters and direct observers to particular locations (Michelsen, Andersen, Storm, Kirchner, & Lindaner, 1992).

The controversy over the interpretation of honeybee waggle dance studies also illustrates the general need to eliminate from social-learning experiments the confounding effects of residual cues left by demonstrators, demonstrator activity in the presence of subjects, and environmental factors (Gould, 1975b, 1976). Moreover, waggle dance studies illustrate how conflicting data can result because social information use can vary between individuals and conditions (Grüter & Farina, 2009; Sherman & Visscher, 2002). The techniques utilized in the study of honeybee social learning could be adapted to other animals, and the increasing number of studies uncovering social learning or social information use in invertebrate species that are relatively easily manipulated in field settings (Laidre, 2010; Leadbeater & Chittka, 2007) suggest that invertebrates will provide much useful information on the ecology of social learning.

Bringing Behavior Into the Laboratory: Laboratory Experiments Based on Field Observations

All laboratory studies of social learning will, to a greater or lesser degree, focus on the typical behavioral repertoire of the species under study. Several studies, however, have directly taken field observations and brought them into the laboratory, even explaining how social learning can facilitate invasion of a new habitat (Terkel, 1996). For example, demonstration of the time and energetic savings for squirrels opening nuts and rats extracting seeds from pine cones with exposure to a trained model illustrate how ecologically relevant laboratory studies can address the function of social learning (Terkel, 1996; Weigl & Hanson, 1980). We discuss some instructive examples of laboratory experiments undertaken explicitly to uncover the mechanisms or functions of acquisition of specific behavior patterns observed in the field. Some demonstrate the necessity of social information for acquisition, whereas others show that social information is not required.

Rats diving for food. Wild rat colonies along the Po river in Italy dive for and feed on mollusks on the river bed, whereas neighboring colonies, where mollusks are also available, do not (Galef, 1980). This patchy pattern could, like regional differences in chimpanzee behavior (Whiten et al., 1999), be explained by a combination of rare individual innovation and social learning within a locality. However, laboratory experiments demonstrated that social learning is not essential for the development of diving behavior (Galef, 1980). Rats were trained to dive for submerged chocolates (a preferred food) by gradually submerging the chocolates in water. Interaction with trained rats did not lead to diving by naive subjects, but rats trained to swim would dive for food, raising the possibility that diving could result from the social learning of swimming. Social interaction accelerated acquisition of swimming in a domestic rat strain, but experiments demonstrated that swimming could develop before adulthood with or without a trained demonstrator, meaning that social learning was not necessary for the development of swimming and, consequently, the development of diving. In a final experiment, rats that regularly dove to retrieve chocolate were shown to stop diving for chocolate if other food was made available, even though chocolate was the preferred food. Galef (1980) suggested that natural shaping, via mollusks being revealed by fluctuations in the water level, could explain the presence of the behavior pattern in at least some wild groups where such fluctuations in water level exist, whereas the availability of alternative food resources could explain its absence in neighboring groups. Moreover, these results suggest further field experiments (Galef, 1980). For example, alternative food resources could be provided to diving populations, with the prediction that diving would cease, whereas nondiving rats could be trapped and tested in the laboratory to determine whether they do not dive because of the availability of other resources.

Primate potato washing. Japanese macaques' (*Macaca fuscata*) washing of sandy food provides a key, although controversial, example of the spread of a novel foraging behavior that some assert is a result of social learning (Hirata, Watanabe, & Kawai, 2001; Kawai, 1965). However, experiments providing sandy food to small captive groups of tufted capuchin monkeys (*Cebus apella*) and crab-eating macaques (*Macaca fascicularis*) showed that the majority of individuals consistently washed sandy food, without evidence of copying (Visalberghi & Fragaszy, 1990). Thus, individual discovery could explain the high frequency of food washing in monkeys, including Japanese macaques. Similarly, a study of grackles dunking food in water, also a proposed example of social learning, revealed that under ideal conditions in captivity, many individuals dunk food, even though the behavior is infrequent in the wild (Morand-Ferron, Lefebvre, Reader, Sol, & Elvin, 2004).

Avian tool use. Observations of tool use and manufacture in woodpecker finches (*Cactospiza pallida*) and New Caledonian crows (*Corvus moneduloides*) led to both considerable interest in the method of acquisition of the behavior and speculation that social learning may be involved (Hunt, 1996; Hunt & Gray, 2004; Kenward, Rutz, Weir, & Kacelnik, 2006; Kenward, Weir, Rutz, & Kacelnik, 2005; Orenstein, 1972; Tebbich, Taborsky, Fessl, & Blomqvist, 2001). However, studies on captive-reared individuals confirmed that social demonstrations of tool manufacture and use were not necessary for tool use to develop (Kenward et al., 2006; Kenward et al., 2005; Tebbich et al., 2001). Such studies illustrate the value of captive studies, in which the prior histories of animals are known and controlled, for understanding processes involved in behavioral development in the wild.

British titmice opening milk bottles. The spread across the United Kingdom of birds opening milk bottles and drinking the cream from the milk surface is often regarded as a classic case of social transmission, although the original investigators were cautious in their interpretation of the process of diffusion (Fisher & Hinde, 1949; Hinde & Fisher, 1951, 1972). Milk bottle opening is certainly the best characterized, and perhaps best known, example of the spread of a novel behavior pattern in nonhuman animals. Over 30 years, ornithologists noted the repeated appearance of birds opening milk bottles at tens of sites and in thousands of birds, although the specific opening technique was variable, even within individuals (Fisher & Hinde, 1949; Hinde & Fisher, 1972).

Captive experiments on titmice and black-capped chickadees (*Poecile atricapilla*) cast doubt on social learning as the sole explanation for the spread of the behavior, demonstrating that the rate of spontaneous opening of milk bottles can be quite high, even in seminatural conditions with animals living together and alternative foods available (Kothbauer-Hellman, 1990; Sherry & Galef, 1984, 1990). The nonsocial origin of milk bottle opening is supported by analyses of the geographical spread of the behavior, which suggested many independent origins (Lefebvre, 1995). However, in chickadees, the rate of learning to open tubs of cream was increased in birds that encountered open food sources (Sherry & Galef, 1984, 1990), demonstrating that at least one form of social learning can play a role in its spread. The most likely explanation for the spread of bottle-opening behavior was local innovation, where milk bottles were introduced, followed by social learning from bird to bird within that locality (Ingram, 1998).

Rat food preference learning. Field observations that wild rat (*Rattus norvegicus*) populations rapidly learn to avoid poisoned bait prompted Galef and colleagues to embark on an extensive and compelling set of laboratory studies on food preference learning, now also the subject of considerable neuroendocrine research (reviewed in, e.g., Choleris, Clipperton-Allen, Phan, & Kavaliers, 2009; Galef, 2002, 2004), These studies revealed that food preferences could be acquired from other individuals by multiple routes, such as pups' learning from the flavor of their mother's milk, by the scent of conspecific breath, by following others to feeding sites, and by preferring sites marked with excretory cues. When combined with a tendency to avoid novel foods, these socially acquired preferences can allow rats to effectively avoid lethal toxins (Noble, Todd, & Tucit, 2001). Field studies of food preference learning would be feasible, but to our knowledge, the definitive experiments have not yet been done. However, studies of wild rats in a large outdoor enclosure created demonstrators by adding cinnamon scent to the head region of marked rats and then presented the colony with feeders containing cinnamon- or peppermint-flavored food (Berdoy, 1994). Cinnamon-flavored food was preferentially consumed, and a control group without demonstrators had no preference for cinnamon- over peppermint-flavored food. Moreover, the demonstrators did not initially eat cinnamon. Thus, with this elegant design, Berdoy was able to introduce demonstrators while excluding the possibility that subjects' cinnamon preference was the result of simultaneous feeding alongside demonstrators.

Birdsong learning. Birdsong is perhaps the best studied example of social learning, with questions of mechanisms, development, adaptive function, and evolution all well represented. We cannot do justice to this vast field here but note some examples where the methodology of song learning could be adopted to study other domains of social learning. Field studies, such as Jenkins (1978), have established that song learning occurs in the field by examining the song match between birds, the distribution of song groups across a habitat, and changes in songs over time, while ruling out a role for genetic inheritance from the father in song production. Moreover, because birds were translocated to a new habitat as part of a reintroduction effort and the same songs were found in the old and new habitats, it is unlikely that birds living in close proximity and sharing songs had individually adapted their songs to a particular locale (Jenkins, 1978).

Both because song is complex and highly variable and contains arbitrary elements and because laboratory studies have demonstrated that birds copy their tutors, spread of songs through populations can be monitored without intrusive experimental tests of social learning (Beecher, 2008; Lynch & Baker, 1994; Slater, 1986). This is a major advantage to social-learning studies based on the vocalizations of both birds and cetaceans. It remains an open question whether other behavior patterns exist that have the characteristics of song that allow social learning to be demonstrated on the basis of the match between the behavior of two or more individuals, although it has been argued that, like bird song, some primate foraging behaviors are complex and highly variable and contain arbitrary elements (Byrne, 2007). However, where acts are rewarded, a match in the behaviors of individuals will not be informative, because animals are likely to independently arrive at similar ways of doing things. Consequently, acquisition of arbitrary acts, such as the choice between two equally rewarding foraging sites (Thornton & Malapert, 2009; Warner, 1990b) or group-specific arbitrary social customs (Nakamura & Uehara, 2004), can be particularly useful in elucidating social learning.

Birdsong studies illustrate several relevant approaches for social-learning research. For example, telemetry can examine what kind of information animals attend to in the field and, hence, can establish likely transmission routes. For example, juvenile song sparrows prefer to "eavesdrop" on song interactions between adults, rather than solo songs, emphasizing how social interactions are important to song learning (Beecher, 2008; C. N. Templeton, Akçay, Campbell, & Beecher, 2010). Playback studies that compare birds' responses to known and unknown songs can be used to determine what birds know (Stoddard, Beecher, Homing, & Campbell, 1991). Similar methods could be adopted to other behavior patterns: Perhaps animals preferentially attend to novel foraging acts, whereas they ignore acts already in their repertoire, or perceive as more salient behaviors occurring in specific social contexts. Birdsong researchers have also successfully combined field and captive studies, controlling the access of individuals to potential demonstrators (e.g., Nordby, Campbell, Burt, & Beecher, 2000; Zann, 1990). For example, Zann captured juvenile finches of different ages and placed them in an enclosure within the source colony, thus precluding close interaction with their fathers. The younger the birds were when they were confined, the less their songs matched those of their fathers, establishing the importance of interaction with the father during the sensitive period for learning his song. Birdsong studies illustrate how the timing, context, and source of social information are important determinants of social learning.

Discussion

Social learning has been experimentally demonstrated in the wild in a range of taxa and a range of contexts. Our survey is probably incomplete but, nonetheless, includes learning of foraging resources, locations, and techniques; responses to predators and brood parasites; travel routes; mating sites; and habitat and nest site choices. Moreover, socially acquired responses have been shown to be long-lasting in wild populations (e.g., Betts et al., 2008; Müller & Cant, in press; Warner, 1988). Social learning is thus both widespread and relevant to animal ecology, and we would argue that, as with many other aspects of ecology, social learning is beneficially studied in situ. Not only are field experiments feasible, they are also a vital part of understanding social learning. Although the number of field experiments has expanded dramatically in recent years, such studies remain relatively rare. Moreover, studies of captive animals (e.g., Kenward et al., 2005; Tebbich et al., 2001) have shown that behavior patterns originally ascribed to social learning may not require social information for their development, which provides a note of caution when population differences in behavior can perhaps be too readily labeled as cultural phenomena without sufficient evidence. That said, the fact that a behavior can develop in the laboratory without social learning does not rule out a role for social learning of that behavior in natural circumstances (Kenward et al., 2006).

Numerous approaches have been taken to study social learning in the field, ranging from manipulations of entire populations to insertion into populations of trained individuals or novel resources, the blocking of transmission avenues, or creating the appearance that animals are performing a particular behavior or choosing one resource over another. Studies of social or public information use could be relatively simply extended to also examine social learning by subsequently testing individuals without demonstrators present; we noted many such missed opportunities in the published literature. Where control populations are not available, baseline measures can be taken or multiple successive tests with altered task demands can be administered, although such “controls” would be less powerful than concurrently tested control groups.

Both field and captive studies contribute to a fuller understanding of the processes of socially mediated learning, but are field studies really essential? Our survey illustrates that they are. Field work has provided evidence for processes not yet demonstrated in the laboratory, such as social learning of brood parasite mobbing or mating sites (Davies & Welbergen, 2009; Warner, 1988), and has produced results contrary to those of laboratory studies (e.g., Gajdon et al., 2004; Lefebvre, 1986). Thus, in some cases, field studies may be more feasible than captive studies and may open new avenues for research in the laboratory, as well as demonstrating that social learning is relevant to the life of wild animals. Rigorous field demonstrations of social learning, its underlying processes, and its adaptive consequences are feasible and essential.

Closing the gap between the laboratory and the wild. Galef and Allen (1995) highlighted how the almost exclusive use of observer–demonstrator pairs in social-learning research, although providing a simple and powerful design for elucidating transmission mechanisms, suffers from being largely unrepresentative of the learning opportunities that animals encounter in the wild. Social animals typically have access to the behavior of multiple potential demonstrators and, outside the laboratory, are also likely to be exposed to a variety of potential resources and techniques for obtaining them. What effect rich physical and social environments have on the (1) emergence of novel behaviors, (2) dynamics of their diffusion among group members, (3) multigenerational survival of traditions, and (4) transfer of knowledge between groups are questions that clearly require a move away from observer–demonstrator pairs toward more ecologically relevant designs, even in captivity (Laland, Richerson, & Boyd, 1993; Whiten & Mesoudi, 2008).

With these criticisms in mind, there has been burgeoning interest in creating captive methodologies that better reflect conditions in the wild. Transmission chain designs (e.g., Curio, Ernst, & Vieth, 1978; Galef & Allen, 1995; Laland & Plotkin, 1992; Laland & Williams, 1997) in which trained demonstrators pass on behavior patterns to observers, who then become demonstrators for the next observers in the chain, are useful for examining the fidelity of transmission and, thus, the potential longevity of traditions. Transmission chains simulate the addition of naive individuals to groups. So-called open group diffusion studies again provide a more naturalistic design than do more rigorously controlled but simpler captive studies (Whiten & Mesoudi, 2008). Diffusion studies replicate situations in which novel behavior patterns are introduced through either innovation or arrival of migrants: Inventions must spread from a single demonstrator through a group, potentially competing with alternative solutions that emerge and spread in the meantime. The fates of such alternative solutions are interesting in themselves and can help determine how the identities of independent innovators influence the transmission versus extinction of behavioral alternatives. Indeed, the innovations of subordinate individuals may represent dead ends in terms of transmission (Bonnie, Horner, Whiten, & de Waal, 2007; Laland & Reader, 1999; Midford et al., 2000; Reader & Laland, 2001), due either to the lack of opportunity of subordinates to perform a behavior (if the resource is limited) or to the low salience of their demonstrations (their behavior is not attended to by fellow group members). Diffusion studies with chimpanzees typically train a high-ranking individual as a demonstrator to reduce such problems (e.g., Whiten et al., 2005). Diffusion studies provide the opportunity to study complex transmission dynamics and are likely to proliferate as an informative, powerful, and ecologically relevant captive design.

Open questions of social learning. Field experiments raise new research questions and also point to routes to address open questions concerning social learning. Field experiments are particularly valuable in addressing the adaptive significance of social learning but can assist in establishing the generality of laboratory findings concerning all four of Tinbergen’s (1963) questions: mechanism, development, adaptive function, and evolution. Although much has been learned through both laboratory and field studies regarding mechanism and function, developmental and evolutionary perspectives remain relatively unexplored. For example, are there sensitive periods for social learning or developmental changes in who and what aspects of behavior individuals attend to? Do individuals specialize in learning individually or socially, and, if so, how does development shape specialization? What selective pressures, if any, drive some species to evolve increased sensitivities to socially acquired information, and what can we learn from identifying informative cases of convergence? Moreover, field experiments can address issues that do not fit neatly into Tinbergen’s scheme, such as the evolutionary consequences of socially acquired traits or the role of social learning in niche construction (Odling-Smee, Laland, & Feldman, 2003; Wyles, Kunkel, & Wilson, 1983).

An obvious question is the taxonomic distribution of social learning. The majority of the studies (12 of 23 studies, 12 of 20 species[4]) in our survey (see Table 1) focused on birds, with fish, social insects, and mammals also represented. Surprisingly, and despite the intense interest in primate social learning (Fragaszy & Perry, 2003), social learning in wild populations of nonhuman primates has been definitively demonstrated experimentally only very recently, and in a single study (van de Waal et al., 2010). Social learning is taxonomically widespread, although whether the same processes are involved in the various instances reported is currently unknown.

The observed taxonomic distribution of animals utilizing social learning will reflect research traditions and the ease of performing field experiments with different taxa, and it remains an open question to what extent ecology versus other species characteristics, such as cognitive ability or social structure, determines species differences in social learning (Lefebvre & Giraldeau, 1996; Lefebvre & Palameta, 1988; Reader & Laland, 2002; Reader & Lefebvre, 2001; J. J. Templeton, Kamil, & Balda, 1999). For example, will social learning be more widespread, faster, or involve different transmission mechanisms among egalitarian species or those with well-defined hierarchical organization (see Kendal, Custance, et al., 2010; Lonsdorf & Bonnie, 2010)? Is the capacity to learn socially an adaptive specialization, or does much social learning result from the by-products of other behavior, such as grouping (van der Post & Hogeweg, 2006)? For example, differences in the social learning of escape routes between wild guppies, domesticated zebrafish (*Danio rerio*), and domesticated guppies may reflect differences in grouping tendencies (Brown & Laland, 2002; Lindeyer & Reader, 2010; Reader et al., 2003). Similarly, local foraging conditions can result in learned preferences for particular conspecific versus heterospecific tutors (Carlier & Lefebvre, 1997; Dolman, Templeton, & Lefebvre, 1996). The extent to which social-learning propensities and preferences to attend to particular demonstrators vary across individuals or are shaped by experience or local conditions in the field is unknown (Kendal, Coolen, van Bergen, & Laland, 2005; Laland, 2004; Leadbeater & Chittka, 2009; Toelch et al., 2009). Indeed, the presence or absence of social learning may not be a species characteristic. Instead, the use of social information may vary across contexts and ecologies, and discovery of novel forms of social learning may be more a matter of designing intelligent experiments than of studying intelligent animals.

Field experiments can also go beyond the issue of whether social information is used to acquire a behavior pattern. For example, several studies have examined the integration of social, individual, and ecological information—notably, work on habitat selection in birds (e.g., Seppänen & Forsman, 2007). The integration of different sources of information, including different sources of social information, is an important issue. For example, the relative utility of a given foraging behavior could be influenced by the availability of other foods, the ease of identifying alternate foods, differences in need (e.g., disease promoting peculiar nutritional requirements), local predation risk, cognitive or other constraints on performance of alternative foraging behaviors, or the activities of others (Dewar, 2004; Reader, 2004). A focus on social learning can lead to neglect of other processes involved in the maintenance of traditions. Traditions depend not just on social acquisition of behavior, but also on its retention; if individuals modify socially acquired behavior or innovate, a tradition is lost (Heyes, 1993). Manipulations of the social environment could help determine the role of both demonstrators and nondemonstrators in the spread of behavior, whereas manipulations of the physical environment could address hypotheses regarding the evolution or function of social learning and the maintenance of traditions.

Finally, field experiments can also address applied issues. For example, it has been suggested that social learning provides a way to increase the success of captive-reared individuals released into the wild, important for both conservation and farming (Griffin, 2004; Suboski & Templeton, 1989). One year after release into the wild, captive-reared black-tailed prairie dogs trained to predators in the presence of experienced adults had almost double the survivorship of juveniles trained without experienced adults (Shier & Owings, 2007), demonstrating that social information can provide a survival advantage, potentially improving conservation programs. Social learning can also be used to train individuals to respond to unfamiliar threats (Griffin, 2004), and manipulation of social cues may therefore facilitate the relocation of problem or impacted species. Under certain conditions, the use of social cues may have maladaptive consequences—for example, when environmental change outpaces traditional behavior. Lastly, local traditions may themselves be the subject of conservation efforts when extinction of a local population destroys local traditions, as well as the individuals exhibiting them (Corten, 2002; van Schaik, 2002; Whitehead, 2010).

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NOTES

1. Humle and Matsuzawa (2002) involved no explicit manipulation of the environment or of individuals.

2. Witte and Ryan (2002) had no test of learning.

3. Matsuzawa et al. (2001) introduced unfamiliar nuts to a nut-cracking population of wild chimpanzees, but the extent to which a suspected model was responsible for the acceptance of the nuts by the rest of the community is unclear in the absence of a control population with no demonstrator.

4. Multiple studies on the same behavior pattern in the same species are counted once.

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