



## Does the house sparrow *Passer domesticus* represent a global model species for egg rejection behavior?

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Conspecific brood parasitism (CP) is a facultative breeding tactic whereby females lay their eggs in the nests of conspecifics. In some species, potential hosts have evolved the ability to identify and reject foreign eggs from their nest. Previous studies suggest that the ubiquitous house sparrow *Passer domesticus* in Spain and South Africa employs both CP and egg rejection, while a population in China does not. Given the species' invasive range expansions, the house sparrow represents a potentially excellent global model system for parasitic egg rejection across variable ecological conditions. We examined the responses of house sparrows to experimental parasitism at three geographically distinct locations (in Israel, North America, and New Zealand) to provide a robust test of how general the findings of the previous studies are. In all three geographic regions egg rejection rates were negligible and not statistically different from background rates of disappearance of control eggs, suggesting that the house sparrow is not a suitable model species for egg rejection experiments on a global scale.

House sparrows *Passer domesticus* are the most geographically widespread birds on Earth. As such, they may represent excellent global models of organismal biology, evolution, and ecology research allowing comparisons of traits across varied contexts. The identification and rejection of foreign eggs from one's nest is a central behavior of interest in the study of avian brood parasitism, and some studies out of Europe and South Africa seem to indicate that the house sparrow engages in this behavior in response to being parasitized by conspecifics. However, a study from China reports a lack of this behavior in a native population, and our new data reported here also demonstrates a similar lack of this behavior in house sparrows across three continents. This calls into question the external validity of egg rejection studies focusing on house sparrows, and suggests that they do not represent a suitable global model species of this behavior.

Avian brood parasitism incurs significant fitness costs on the host and is a strong selective pressure favoring the evolution of antiparasitic defensive strategies (Davies and Brooke 1989, Begum et al. 2012). One of the most common and effective countermeasures that hosts employ is the recognition and rejection of foreign eggs, usually by detecting differences in eggshell coloration and maculation between their own eggs and foreign eggs (Hauber et al. 2015).

In addition to interspecific brood parasitism (IP), studied most extensively in common cuckoos *Cuculus canorus*,

conspecific brood parasitism (CP) is a facultative strategy in which females lay their eggs in conspecific nests (Davies 2000). CP offers several key advantages to parasites over interspecific parasitism, including ease of nest access and 'instant' egg mimicry, and has been reported in over 250 bird species (Lyon and Eadie 2008). Counter-adaptations to CP are rare (Samas et al. 2014), as the naturally 'mimetic' conspecific eggshells may represent a perceptual difficulty in foreign egg discrimination. Also, CP typically inflicts less of a fitness cost on the host than some obligate, interspecific brood parasites: while a host in an instance of CP pays a cost for caring for a typically unrelated individual, a host in an instance of IP suffers the same cost as well as the potentially higher cost of the death of its own chicks (e.g. via eviction of host progeny by obligate parasitic hatchlings; Grim et al. 2009). Yet, some hosts have evolved a fine-tuned discrimination ability even against very similar conspecific eggs, including nest desertion and selective egg rejection (Grendstad et al. 1999, Lyon 2003, Samas et al. 2014). Nonetheless, experimental studies of CP remain rare, especially compared to a massive research effort invested into the study of IP (Grim 2007).

One species that has been shown to employ CP is the house sparrow *Passer domesticus* (Kendra et al. 1988). Due to its global range (Anderson 2006), the species represents an opportunity to study parasite-host dynamics and behavioral responses over vastly variable environmental and social

conditions. In fact, its ubiquity makes the house sparrow a potential model species for studying global egg rejection behavior. However, conflicting results found in the literature call this suitability into question.

Here we examined whether house sparrows are indeed a suitable ecological and experimental model for egg rejection studies by comparing new data from three geographically distinct populations with published data on foreign egg rejection patterns. Such data include findings from the introduced population on Dassen Island, South Africa subjected to artificial parasitism (wherein a foreign conspecific egg was introduced to nests by an experimenter either in addition to existing eggs or by replacing an existing egg) exhibited a relatively high rate of foreign egg rejection (24–46%) (López de Hierro and Ryan 2008).

Two more recent reports on a captive native population in Granada, Spain showed similarly high rejection rates in artificially parasitized sparrow nests (27–33 and 44% of foreign eggs rejected, respectively; López de Hierro and Moreno-Rueda 2010, Soler et al. 2011). The 2010 study in particular provided data on differential host responses to treatments of the introduced egg, either variable size or manipulation of the shell color/spot pattern. Introduced eggs with variable brown spot patterns (i.e. 'mimetic' eggs with manipulated maculation) produced a significantly higher rejection rate than those that were of a different color. In contrast, Soler et al. (2013) also in Granada, Spain, reported a baseline rejection rate of 30% for artificially colored (red) eggs but a 0% rejection rate for spotted eggs in a corresponding experimental design (see: 'experimental group 2' vs baseline experiment in Soler et al. 2013).

López de Hierro and Moreno-Rueda (2010) also made reference to an artificial parasitism study on a wild introduced North American population of house sparrows by Kendra et al. (1988), citing a 35% rejection rate comparable to their own reported findings. However, the 1988 study reveals rather that 35% of individuals responded in some way to the experimental manipulation, most by skipping an egg-laying cycle and only one individual (6%) actively ejected eggs from her nest according to the definition of egg rejection adopted in our study and in other studies we review here (see Methods).

The propensity for CPB and egg rejection has yet to be studied in many other populations of house sparrows in distant sites and diverse ecosystems, both native and introduced, and both in captivity and in the wild. A recent study by Yang et al. (2015) represents the first examination of a native Asian population in this regard, subjecting a freely breeding population in northwestern China to artificial parasitism. Here, the researchers placed either clay model eggs or painted natural sparrow eggs (either completely red or spotted with brown blotches) into nests within newly laid clutches, expecting rejection rates resembling the 2010 Granada study to which their protocol was comparable. They found a near total absence of rejection behavior regardless of the type of experimental manipulation. These authors speculated that this discrepancy could potentially be attributed to an evolutionary equilibrium by which their study population had lost rejection behavior to avoid the high cost of collateral own-egg loss demonstrated in the European and South African studies.

Within any host of avian brood parasites there might be spatial and temporal variations in particular biological traits, including egg rejection rate; indeed, such geographic variation was detected in almost all studies that examined multiple host populations in the context of brood parasitism and egg rejection (Soler et al. 1999, Stokke et al. 2008, Polačiková and Grim 2010, Grim et al. 2011, Samas et al. 2014). A critical way to establish the generality of patterns in biology is metareplication, i.e. replication of whole studies across time, space and phylogeny (theory: Johnson 2002, empirical examples: Davies and Brooke 1989, Moksnes et al. 1991, Lahti 2005, Polačiková and Grim 2010, Grim et al. 2011, Samas et al. 2014). Another fundamental aspect of biological study design is the biological and statistical independence of the samples (Hurlbert 1984). Thus, we combine evidence from three new studies from three widely separated geographic regions of the world. This was made possible by previous human-assisted introductions of house sparrows. Such model systems and species may be ideal for studying fundamental coevolutionary questions that are impossible to address in native host ranges (Grim and Stokke 2016).

Here we mirrored the protocols of López de Hierro and Moreno-Rueda (2010) and Yang et al. (2015) to experimentally test egg rejection among house sparrows breeding in wild in the continental USA and New Zealand and in captivity in Israel. We then examined our data in relation to prior studies to assess the relationship of population history (native/introduced) and breeding type (wild/captive) upon egg rejection prevalence and the suitability of the House Sparrow species as a global model species of egg rejection behavior.

## Methods

### Israel study

Experiments were conducted on the house sparrow colony in the zoological gardens of Tel-Aviv Univ. (for more details, see Grodzinski et al. 2009), where individuals were kept in aviaries. The birds were provided with nest boxes, nest-building materials, sand for dust baths, mealworms *Tenebrio molitor* and ad libitum with water, seed mix and dry insect mash. The study was carried out during the breeding season of 2010. Nest boxes were monitored on a daily basis, information on the nest-building process, laying date, clutch size and evidence for possible instances of CP was gathered. As the house sparrow lays one egg every 24 h, background levels of CP were inferred if there was an appearance of two new eggs at the same day (Yom-Tov 1980).

For the manipulation, the experimental eggs ( $n = 38$ ) were inserted into host nests during the third or fourth morning of egg laying (i.e. after the host has laid its third or fourth egg). Each nest was artificially parasitized once and eggs were introduced both via the egg exchange method (exchanging one of the eggs with an experimental egg,  $n = 21$ ) and the egg introduction method (adding an experimental egg to the clutch,  $n = 17$ ). The experimental eggs were fresh natural conspecific eggs taken from other nests in the same colony. Furthermore, since various studies have shown that acceptance and rejection of the parasitic egg may

vary throughout the course of the breeding season (Lotem et al. 1992, 1995, Brooke et al. 1998), the experimental eggs were introduced throughout the breeding season to capture the potential variation in egg rejection behaviors.

Natural sparrow eggs were modified to form three different variants of foreign, 'parasitic' eggs (Fig. 1): dark brown painted eggs ( $n = 6$ ), light brown painted eggs ( $n = 4$ ), and natural eggs with dark brown spots painted ( $n = 21$ ). The egg features were modified using an acrylic non-toxic paint (Decoart ©-Asphaltum DA180 and Cool White DA240). Seven unpainted eggs were also used (and never rejected), but were removed from analysis to allow comparisons with the other datasets from USA and New Zealand where such eggs were not used. After the introduction of the parasitic egg, nests were checked for rejection on a daily basis. Rejection was noted when the foreign egg was missing from the nest ('ejection') or was found buried under nesting material ('burial'; López de Hierro and Moreno-Rueda 2010). An egg was considered 'accepted' if it remained in the nest at least

for 6 d after the start of the experiment (Lotem et al. 1995). Nests were also monitored in order to determine hatching and breeding success, thus in practice we could also detect egg rejection had it occurred after the six days criterion (which did not happen).

### Continental USA study

In 2013, we originated The House Sparrow Project, a citizen science program in which volunteers who regularly monitor birds nesting in boxes across the lower continental USA, North America, carried out a standardized experimental protocol with house sparrow eggs (for more details, see Larson et al. 2016). Volunteers reported on 114 house sparrow nests in 16 different geographic localities. For a given nest, participants began the experiment when at least three eggs were already laid. Volunteers labeled each egg with a number at the sharp pole, and carried out one of three randomly assigned treatments: all brown, all red, or 20 brown spots. In

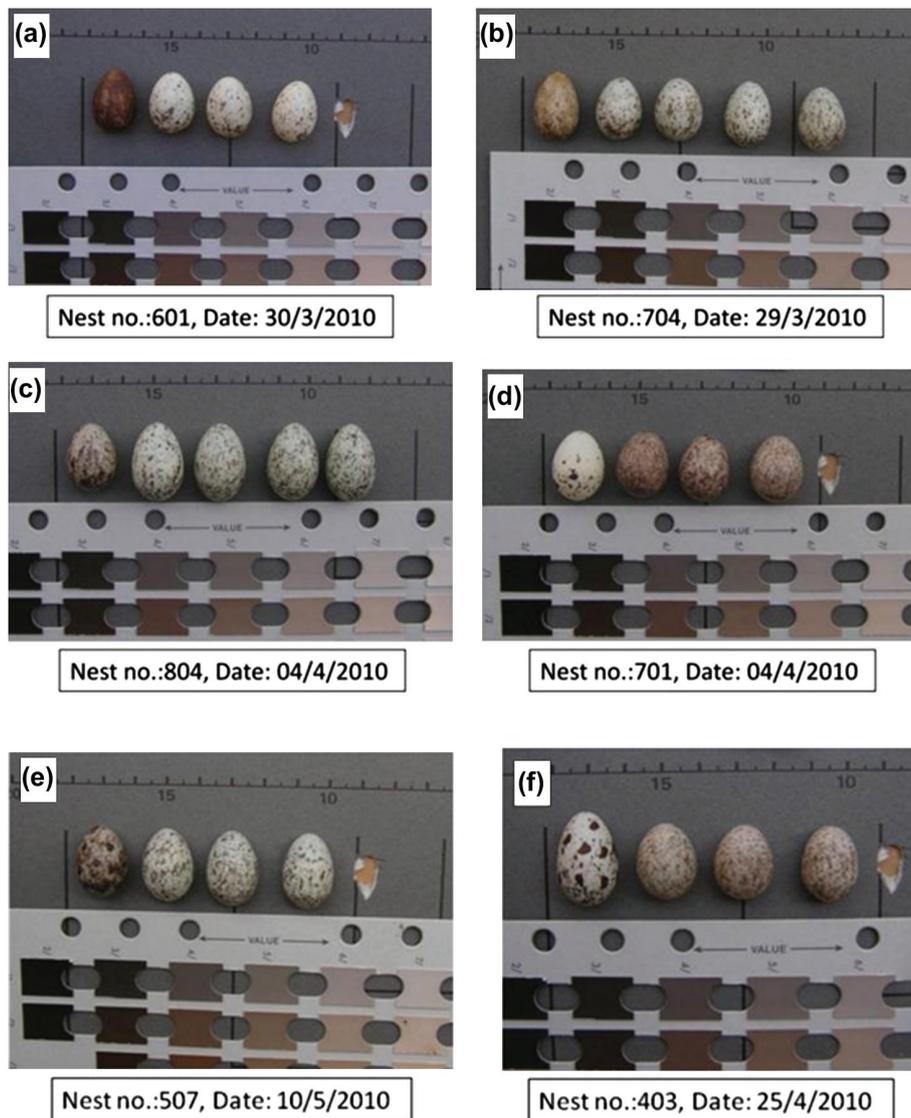


Figure 1. Experimentally modified real house sparrow eggs used in the Israel study. (a) Dark color painted eggs, (b) diluted color painted eggs, (c) unpainted dark variant (removed from analysis), (d) unpainted bright variant (removed from analysis), (e) and (f) natural eggs with dark brown spots.

the all brown and all red treatments, one egg was chosen at random and painted completely using a felt-tip marker pen (Prismacolor™). In the 20 brown spots treatment, one egg was chosen at random and painted with twenty brown spots, each approximately 5 mm in diameter (Fig. 2).

As a ‘manipulated control’, in addition to one of the experimental treatments, one egg (other than the experimental egg) was chosen and painted all over with a Prismacolor™ Premier colorless blender, which is a pen type containing the solvent found in the other two pen types, but not the pigment. Eggs handled in the same way as manipulated eggs (experimental and control) but not painted served as ‘unmanipulated controls’.

An egg was considered accepted if it was present in an active nest for at least 6 d after the treatment was applied; this threshold has been used in the study of both interspecific (Lotem et al. 1995) and conspecific parasitism (Samas et al. 2014). Nests were monitored every 1–2 d until eggs were considered accepted or rejected. An egg was considered rejected if the egg went missing from the nest. At each monitoring visit, all eggs were removed, and manually checked for possible signs of breakage and then returned to the nest. Any new eggs were numbered, and any egg losses were noted. Eggs that were broken by the experimenter, and eggs in nests that were abandoned or depredated were removed from the analyses.

### New Zealand study

Experiments took place between November 2012 and January 2013 in the car park of the Miranda Naturalist’s Trust on the Firth of Thames, North Island, New Zealand. Sparrows nested in dense bushes, rather than in cavities, and built free-standing nest structures at this site. We located clutches (n = 40) in active nests (n = 31) by visually searching and following adults carrying nesting material; some nests had multiple successive clutches laid in them. A new clutch was deemed to have been started if the nest was found empty between two visits where it contained eggs, or if all marked eggs were absent from a nest, and replaced with new eggs.

Three egg treatments were used, and randomly selected for each clutch. In the all-brown treatment, one egg was

chosen and painted completely brown using a Sharpie™ brown marker pen. Other eggs in the same clutch were numbered at the sharp pole using a marker to allow identification of individual eggs. In the 20-spot treatment, one egg was chosen and painted with 20 brown spots with the same color marker as above. Other eggs in the clutch were numbered as in the all brown treatment. In the control treatment, one egg was chosen and painted all over with an Artline™ colorless blender, which is a pen containing the solvent but not the pigments found in the other pens. The chosen egg and all others in the clutch were numbered as in the all brown and 20-spot treatments.

In nests with the clutch completed (i.e. same number of eggs in two consecutive days), one egg was chosen at random to be the treated egg. For nests where laying was incomplete, some were selected at the time of discovery to have a subsequent egg be the experimentally treated egg in an attempt to keep the probable proportions of treated eggs even with respect to laying order. Nests were monitored until nest failure or fledging of chicks. At each monitoring visit, all eggs were removed from the nest. Any new eggs were numbered, treated or both, and any egg losses were noted. Any eggs present in an active nest for 6 or more days were deemed ‘accepted’ (Lotem et al. 1995), and any egg lost from the nest within that time was deemed ‘rejected’.

### Statistical analyses

For each set of experiments, a general linear model (GLM) was generated to determine any difference between the rejection rates from our treatment groups. We aimed to determine whether the rejection of a manipulated egg differs from the background disappearance of control eggs. Similar comparisons were also carried out comparing our datasets to each other as well as to previously published reports from various authors and countries. A logistic regression was attempted to compare previous studies with regard to location, native/introduced status, and captivity, but collinearities between geographic and ecological contexts (native vs introduced, captive vs wild) caused the model to fail to fit; this is because there were no captive studies conducted in the introduced regions of the species distribution.

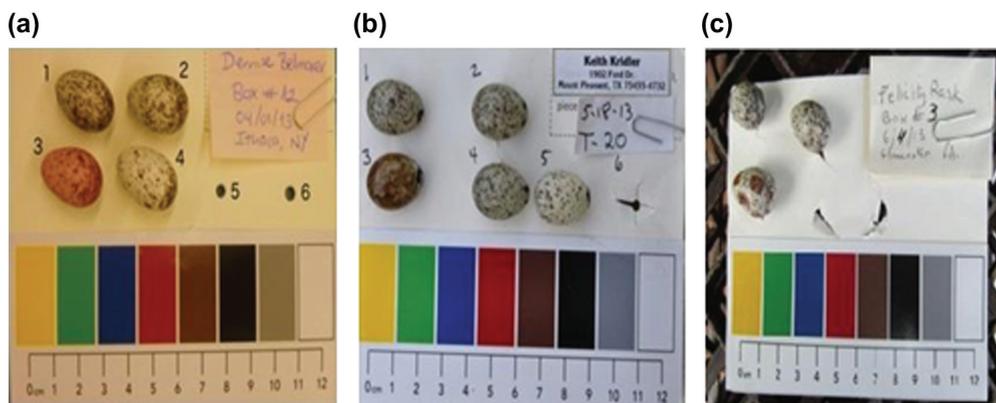


Figure 2. House sparrow eggs on color cards experimentally modified by volunteers in the House Sparrow Project across the continental US. (a) The all red treatment (egg 3), (b) the all brown treatment (egg 3), (c) 20 brown spots treatment (bottom egg). In all images egg 2 was covered with a clear marker (control treatment).

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.16r35>> (Manna et al. 2016).

## Results

### Israel study

There were no instances of two eggs being laid on the same day; thus, no behaviorally detectable cases of CP were observed. Furthermore, out of the 31 nests that were artificially parasitized, no introduced eggs were rejected (i.e. eggs were retained regardless of treatment, Fig. 3a).

### Continental USA study

Overall, from 111 experimental nests, a total of 9 rejections (8.1%) occurred. No significant differences were detected

between the experimental treatment types (all brown, all red, and 20 brown spots) (GLM:  $F_{2,108} = 0.43$ ,  $p = 0.65$ , Fig. 3b). Overall, there were no significant differences in rejection rates between the experimental eggs (regardless of treatment), control eggs, and other eggs in the nest (GLM:  $F_{2,326} = 0.32$ ,  $p = 0.72$ , Fig. 3c).

### New Zealand study

Overall, from 35 experimental nests, a total of 3 rejections (8.6%) occurred. There was no significant effect of treatment type (all brown, 20 brown spots, and control) on the rejection rate ( $F_{2,32} = 0.05$ ,  $p = 0.96$ , Fig. 3d).

### Combined analyses

There were no significant locality-based differences across our three datasets with regard to rejection rate of experimental eggs (GLM:  $F_{2,174} = 1.37$ ,  $p = 0.26$ ). Combining our data

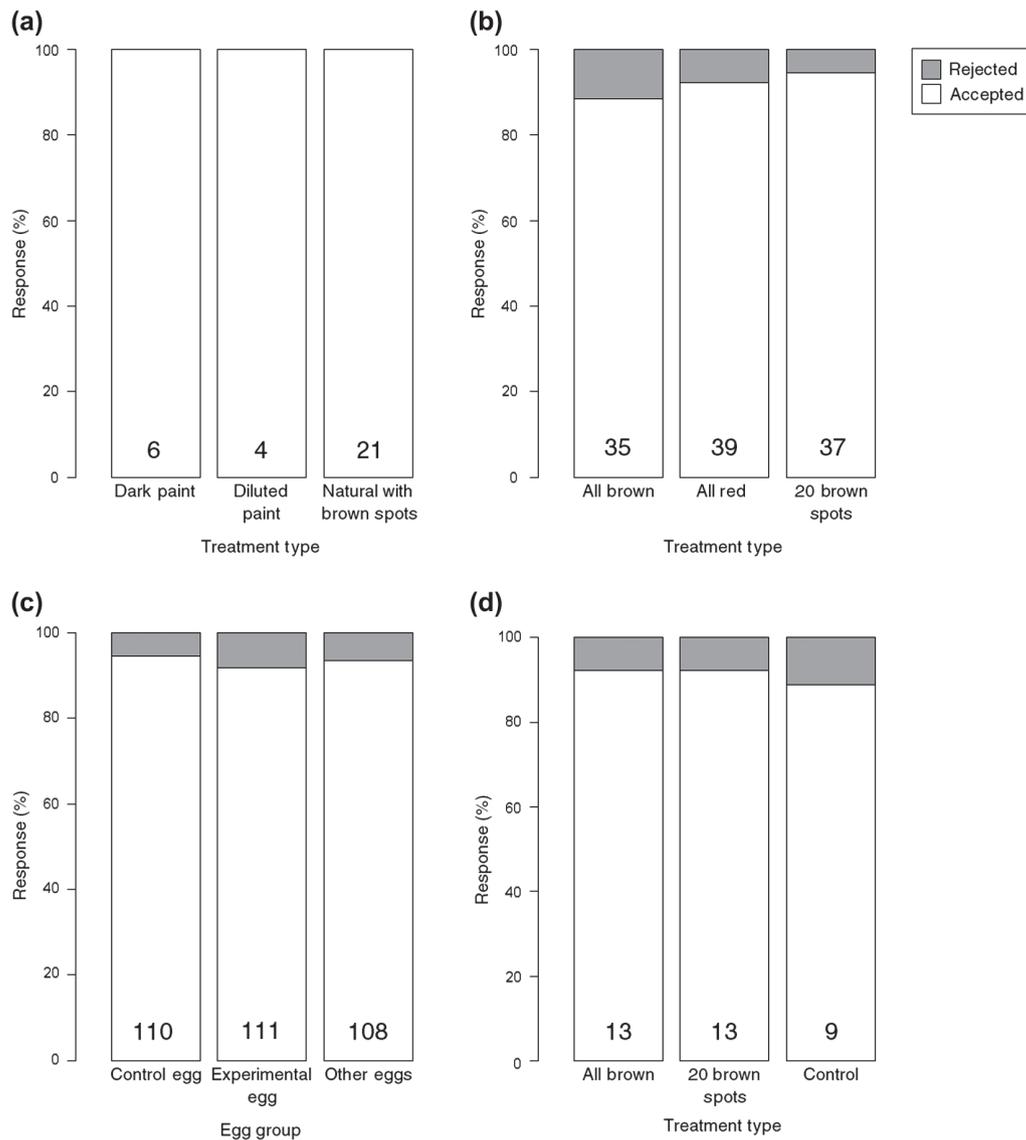


Figure 3. Host responses to experimental parasitism across global geographic scale: (a) data from Israel, (b) data from individual experimental treatments in the continental USA, (c) overall data from the continental USA, and (d) data from New Zealand. Sample sizes are displayed in each bar. For appearance of eggs used in various treatments see Fig. 1 and 2. For details see Methods.

Table 1. Experimental egg rejection rates with sample size, native vs. introduced status, and wild vs captive status across various egg rejection studies of the house sparrow.

Dataset	Population status	Captivity status	n	Rejection rate (%)
USA (this study)	Introduced	Wild	111	8.1
Israel (this study)	Native	Captive	31	0
New Zealand (this study)	Introduced	Wild	35	8.6
Yang et al. 2015	Native	Wild	45	0
Moreno-Rueda and Soler 2001	Native	Captive	62	27.4
López de Hierro and Ryan 2008	Introduced	Wild	27	33
López de Hierro and Moreno-Rueda 2010	Native	Captive	80	28.8
Soler et al. 2011	Native	Captive	52	46.2
Soler et al. 2013	Native	Captive	112	14.3

with those of Yang et al. (2015) also yielded no significant effect of dataset on egg rejection rate (GLM:  $F_{3,218} = 2.23$ ,  $p = 0.09$ ). However, studies in Spain and South Africa reported higher rejection rates (Table 1). Combining our data across all of the previous studies revealed a significant effect of the source of dataset on reported rejection rates of the experimental egg ( $F_{8,546} = 9.659$ ,  $p < 0.01$ ).

## Discussion

House sparrows in all of our three independent and geographically isolated study sites demonstrated very low or absent egg rejection. Furthermore, rejection rates did not statistically differ between experimental eggs and control eggs. This implies a lack of foreign-egg discrimination behavior in our disparate house sparrow study populations. The highest rejection rate here was 11.4% for the all brown treatment eggs in the continental USA study, but even this rate was lower than the 27–35% reported in the 2010 Granada study and statistically not different from the background pattern of egg disappearance of control eggs across the continental USA population. In fact, whereas the previous authors found the strongest rejection response to manipulating the maculation pattern of house sparrow eggs artificially (López de Hierro and Moreno-Rueda 2010), our continental USA dataset's lowest rejection rate was in this treatment (5.4%).

A conceivable explanation for the discrepancies between our data sets and the 2010 Granada study is that two of our populations are wild and introduced whereas the Granada population is captive and native. However, our Israel data were collected from a captive population within the native range of house sparrows, and thus represent the most direct comparison with the Granada study, and yet it showed the lowest rejection rate of all three new data sets (complete absence). Relative breeding density and therefore risk of CP may be a contributing factor to anti-parasitic behavior (Samas et al. 2014), and indeed our Israel population was bred at a low density (not all nest boxes were used and no instances of CP were detected), suggesting a possible explanation for the discrepancies between our Israel data and the Granada data sourced from a high density population with high rates of CP. Yet this argument is once again challenged by the high recognition/rejection rates out of the South African study, which appear to have occurred under low CP risk (López de Hierro and Ryan 2008).

Furthermore, the South African study shows high rates of discrimination and rejection behavior in a wild introduced population, whereas our study showed little rejection in wild introduced populations in USA and New Zealand, also arguing against a relationship between rejection behavior and introduced status. It is likely instead that the different statistical results of these studies and ours are a matter of methodology and definitions. For instance, in their study, López de Hierro and Moreno-Rueda (2010) considered a foreign egg 'accepted' only when it remained in the nest until at least one egg in that brood hatched. All other circumstances that may lead to a brood failing to produce hatchlings were considered an identification and direct rejection of the foreign egg by the host female. In our studies, we focused only on selective egg ejection.

Our USA and New Zealand data show no significant difference in rejection rates between foreign, control, and own eggs in the few cases where rejection did occur, suggesting a high reproductive cost of this behavior as it resulted in collateral own-egg loss. However, the reported relationship between rejection rate and rejection cost is not consistent in the literature, as two studies on the same captive population in Granada produced two very different estimates of rejection costs, from almost half (44.4%) of own eggs destroyed to almost none (4.1%), and yet the reported foreign egg rejection rates were 26–30% and 44% respectively (see Moreno-Rueda and Soler 2001 vs Soler et al. 2011 respectively).

Comparing the published data with our own from across Europe, Australasia, and Africa suggests two conclusions. First, no direct explanation exists regarding native/introduced status or captive/wild studies for why egg rejection behavior seems regionally restricted in house sparrows. Second, in general, egg rejection behavior can now be considered rare in most studied populations of sparrows, thereby rendering this species unsuitable as a global model species for the evolution, development, and plasticity of antiparasitic defenses at the egg rejection stage.

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