



Host–parasite contact and sensitivity to parasitism predict clutch abandonment in cowbird hosts

Christina Petalas^{a,*}, Antoine Turcotte-van de Rydt^b, Simon Ducatez^c,
Mélanie F. Guigueno^b

^a Department of Natural Resource Sciences, McGill University, Montreal, QC, Canada

^b Department of Biology, McGill University, Montreal, QC, Canada

^c Institut de Recherche pour le Développement (IRD) – UMR 241 EIO (UPF, IRD, Ifremer, ILM), Tahiti, French Polynesia

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Abandoning a brood to maximize lifetime reproductive success may result from the current costs affecting future reproductive opportunities. In certain contexts, clutch abandonment can be an evolved breeding strategy rather than a generalized response to stressors such as inclement weather and predation. Obligate brood parasitism, a reproductive strategy in which a parasitic species relies solely on other species to raise its young, imposes fitness costs to hosts and could serve as a trigger for clutch abandonment. This cost, and the resulting clutch abandonment strategy, may vary according to contact with the parasite, sensitivity to parasitism and the value of the current reproductive effort (i.e. brood value). We conducted a phylogenetically controlled meta-analysis covering 85 host species of the three generalist cowbird species (*Molothrus* sp.) in which we examined the following effects on the abandonment (nest desertion and egg burial) of parasitized versus unparasitized clutches: habitat at a small scale (higher host–parasite encounter frequency in open versus forested habitats) and at a large scale (longer interaction between parasites and hosts in prairie versus nonprairie regions), brood value (relative value of a clutch) and host species sensitivity to brood parasitism (relative body mass). Parasitism increased clutch abandonment overall. This increase was strongest in open nonforested habitats, with smaller, more sensitive hosts being more likely to abandon their clutch. Brood value and occurrence in prairie regions did not affect clutch abandonment, indicating that recent, more fine-scale host–parasite interactions were more important than coevolutionary history. Therefore, the abandonment of a brood can be used in diverse parental care strategies, including antiparasitic defences of brood-parasitic hosts.

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Fitness trade-offs are based on the concept that individuals have limited available resources to allocate to competing functions or structures (Haave-Audet et al., 2022; Santos and Nakagawa, 2012). The costs of current reproduction and parental care to future survival and reproductive opportunities are some of the most widely studied fitness trade-offs, fundamental in understanding life history evolution (Harshman & Zera, 2007; Linden & Møller, 1989; Nilsson & Svensson, 1996). If the reproductive value of a brood is outweighed by the cost of providing for the brood, parents may abandon their offspring to focus on future reproductive output, ultimately maximizing their lifetime reproductive success (Zuckerman et al., 2014). Parental abandonment of a brood has

been largely observed across taxa, most notably in birds (Rothstein, 1975; Tobias et al., 2020).

Clutch abandonment can be triggered by different cues. Predation (Lima, 2009), harsh weather (Bottitta et al., 2003) and poor body condition (Spée et al., 2010) are well-established factors that generally elicit clutch abandonment. For example, waterfowl often abandon their offspring after partial nest predation (Ackerman et al., 2003; Armstrong & Robertson, 1988). However, clutch abandonment cues may also be subtler, involving mechanisms such as ‘selective abortion’ of the last-laid egg or improper concealment of nests from predators (Beckmann & Martin, 2016; Kloskowski, 2019). Under certain conditions, clutch abandonment can be a strategic response that allows parents to lay a new clutch in potentially better conditions, thereby increasing their reproductive success within a breeding season or across their lifetime (Bokony et al., 2009; Guigueno & Sealy, 2010).

* Corresponding author.

E-mail address: christina.petalas@mail.mcgill.ca (C. Petalas).

Avian brood parasitism constitutes a strong model to study questions of parental care. Approximately 100 bird species are obligate avian brood parasites, exclusively laying their eggs in nests of other species (Feeney et al., 2014; Soler, 2017). About 10% of all bird species are known to be parasitized (~950 species) by obligate brood parasites (Davies, 2010). Parasitism often imposes an immediate cost on the host's reproductive success as they are required to simultaneously raise both the parasite offspring and their own young or only raise the parasitic young (Medina & Langmore, 2015). The reproductive cost of caring for a parasite selects for, in some hosts, antiparasitic defences that reduce the fitness costs of being parasitized (Feeney et al., 2014). A diversity of host antiparasitic defences exist (Davies, 2010; Peer et al., 2005), including grasping the parasitic egg and ejecting it from the nest (Servedio & Hauber, 2006) or puncturing the parasitic egg (Sealy, 1996). However, these strategies are relatively uncommon, especially among hosts of brood-parasitic cowbirds (*Molothrus* sp.) in the Americas. This is attributed to the shorter period that cowbird hosts have had compared to cuckoo hosts to develop antiparasitic strategies (i.e. evolutionary lag hypothesis; Rothstein, 1975). In addition, many cowbird hosts are small relative to their parasite. They are either constrained by gape size (Guigueno & Sealy, 2011), incur high risks of damaging their eggs in the process of rejecting the parasitic egg (Sealy, 1996; Underwood & Sealy, 2006), or rely on more costly methods of rejecting their parasitized clutch, such as clutch abandonment. Clutch abandonment has been recorded in parasitized clutches (e.g. Clark & Robertson, 1981; Guigueno & Sealy, 2009; Mark & Rubenstein, 2013; Moskát & Honza, 2002; Sealy, 1995), although its probability is highly variable across species (Soler et al., 2015). It is unclear whether clutch abandonment is a direct response to brood parasitism like egg ejection or a more general response to external stresses such as inclement weather or predation risk (but see Hosoi & Rothstein, 2000).

Hormones play a crucial role in modulating behavioural decisions, particularly in response to environmental stressors like brood parasitism (Ruiz-Raya et al., 2018). Specifically, the glucocorticoid hormone, corticosterone, is a key regulator of avian behaviours in response to parasitism (Ouyang et al., 2012; Turcottevan de Rydt et al., 2022). For instance, Abolins-Abols and Hauber (2020) experimentally manipulated corticosterone levels in egg grasp-ejecting American robins, *Turdus migratorius*, and found that parasitized clutches were more likely to be accepted when potential increases in baseline corticosterone levels were inhibited. Thus, mounting evidence suggests that clutch abandonment decisions may indeed be influenced by changes in environmental conditions, such as brood parasitism.

Unlike the extensively studied common cuckoos, *Cuculus canorus*, *Molothrus* cowbird nestlings typically do not evict host eggs or nestlings from the parasitized nest and have a comparatively lower fitness cost for their over 300 hosts (Feeney et al., 2014). The cues that elicit clutch abandonment through nest desertion or burial (laying a new clutch on a superimposed nest) as an antiparasitic response remain unclear (Avilés, 2018; Kosciuch et al., 2006; Lowther, 2018; Manna et al., 2017). Clutch abandonment may be influenced by a variety of factors, including host life history, which should determine the cost of abandoning a clutch versus raising a parasitized one (Servedio and Hauber, 2006), and the coevolutionary history of the host and parasite, which likely determines the degree of adaptation to parasitism (Abolins-Abols & Hauber, 2020).

By performing a phylogenetically controlled meta-analysis, we aimed to disentangle how host life history traits, current exposure to parasitism and the coevolutionary history between host and parasites have shaped clutch abandonment frequencies in cowbird hosts and whether clutch abandonment can be an antiparasitic defence. Specifically, we gathered data from the literature on clutch

abandonment in hosts parasitized by all generalist obligate brood parasite cowbird species, alongside clutch abandonment data from unparasitized clutches as controls. Parasitic species included the North American brown-headed cowbird, *Molothrus ater*, the South American shiny cowbird, *Molothrus bonariensis*, and the Central American bronzed cowbird, *Molothrus aeneus*, which make up all the generalist cowbird species.

First, we examined the level of interaction between cowbirds and their hosts based on breeding range and nesting habitat. Host species that have coevolved with cowbirds for a longer period may have had more time to adapt and fine-tune their response mechanisms, resulting in stronger responses to parasitism (Rothstein, 1975). The history of host exposure to cowbird parasitism varies according to both the host's range and habitat type. The brown-headed cowbird (Røskaft et al., 2002), the shiny cowbird (Mayfield, 1965) and the bronzed cowbird (Cruz et al., 1985) are historically prairie species, but their ranges have expanded beyond the prairies due to habitat modification such as deforestation and agriculture (Kostecke et al., 2004; Røskaft et al., 2002; Smith et al., 2000). Nonprairie bird species are now exposed to cowbird parasitism while potentially lacking the adaptations and experience to effectively respond. On a smaller scale, cowbirds are open-habitat birds that primarily search for hosts in these habitats (Røskaft et al., 2002), making forest-dwelling species less exposed to cowbird parasitism than open-habitat species (Kostecke et al., 2004). However, habitat fragmentation resulting from agriculture and urbanization can increase the presence of cowbirds in forest habitats (Chace et al., 2005). We hypothesized that hosts sharing a longer coevolutionary experience with cowbirds and those with more interactions with cowbirds during the breeding season would be most likely to abandon their clutch.

We also examined the value of a given brood for each host species. In some species, a given clutch represents a high proportion of the lifetime reproductive effort, and each brood has a high value. Abandoning a single clutch, even if parasitized, may then come at a cost that cannot be compensated for with future reproduction. Clutch abandonment may therefore be uncommon in these species. In contrast, for species that spread their reproductive effort across multiple events, and have a lower brood value, the cost of abandoning a parasitized clutch may quickly be compensated for by the benefits of future reproduction, so that these species may benefit from abandoning parasitized clutches. We expected that host species with a high brood value (Bokony et al., 2009) would be less likely to abandon their clutch, as the cost of abandonment would be greater.

Finally, we expected a higher frequency of clutch abandonment in more sensitive hosts, those with smaller body mass relative to cowbirds (Hosoi & Rothstein, 2000). Host species that are smaller than the parasitic cowbird have young that are less able to outcompete the larger parasite nestling for food and space in the nest, thus compromising their survival (Hosoi & Rothstein, 2000). In summary, we predicted that smaller hosts, more sensitive to brood parasitism, would show a higher frequency of clutch abandonment.

By conducting this large-scale phylogenetically controlled meta-analysis across *Molothrus* sp. hosts, we aim to provide a robust analysis determining whether brood parasitism can trigger clutch abandonment as a parental care strategy.

METHODS

Systematic Literature Search

We conducted a literature search of empirical studies that provided counts of nest desertion or egg burial by a host after natural parasitism by any cowbird species (*Molothrus* sp.). We

defined 'nest desertion' as the abandonment of the clutch and nest site and 'egg burial' as the abandonment of the clutch only because a new clutch is built superimposed on the previous nest and eggs, thus still using the same nest site (Guigueno & Sealy, 2010). We first searched both the Web of Science and Scopus publication databases, compiling a comprehensive and replicable screening approach, with the following terms: ('brood parasitism*' AND 'cowbird*'), ('clutch abandonment' AND 'cowbird*'), ('cowbird*' AND 'nest desertion'), ('cowbird*' AND 'abandonment*'), ('cowbird*' AND 'response'), ('nesting success' AND 'cowbird*'), ('natural parasitism' AND 'cowbird*'), NOT ('cuckoo'), yielding a total of 1543 records (including records found in both databases). Subsequent searches were conducted iteratively following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines (see details of each screening iteration in Supplementary Fig. S1) (Moher et al., 2015), resulting in a total of 100 articles included in the analyses. We found an additional 125 records from back-reference searching. A single study could yield more than one data point because breeding success due to parasitism was often determined for multiple hosts in a location. All unparasitized clutch data were obtained from studies that also had reports of parasitized clutches. The literature search was completed in June 2022.

We screened titles and abstracts of the 1543 records and, after exclusions and duplicate removal, assessed full-text articles for eligibility of 1219 peer-reviewed records. To be included the following criteria had to be met.

(1) Parasitized host(s) is a host(s) of a cowbird species that is known to have reared cowbird young successfully (known as 'common' hosts; confirmed using Lowther, 2018).

(2) Parasitized host(s) do not use grasp-ejection or egg puncturing as an antiparasitic defence behaviour but either accept or reject cowbird eggs through burial or desertion (Billerman et al., 2020).

(3) Reports on the incidence of and response to natural parasitism (all experimental parasitism studies were excluded) including the number of naturally parasitized nests and clutch abandonments by either desertion or burial after a confirmed natural parasitism event.

Once a study met the above criteria, we extracted the proportion of abandoned clutches (due to nest desertion and/or burial) in parasitized and unparasitized (if reported) host nests. Life history and habitat information on host species were extracted from the Birds of the World Web site (Billerman et al., 2020). This included a sensitivity categorization based on each host and parasite species' mean body mass. In line with Hosoi and Rothstein (2000), we used 13 g as the threshold body mass above which we considered species as having little sensitivity because of their large size, and below which we considered species as small and with high sensitivity (Hosoi & Rothstein, 2000). Based on distribution maps, we also determined the presence/absence of each host species in the prairie during the breeding season (breeding range), expected to reflect past host exposure to parasitism, and its use of forest versus non-forest as breeding habitat, expected to reflect current exposure to cowbird parasitism.

For each host species, we extracted trait values from the database provided by Sol et al. (2016) to calculate the brood value according to the following formula (Bokony et al., 2009): $\log((\text{clutch size})/(\text{clutch size} \times \text{broods per year} \times \text{maximum reproductive life span}))$.

We decided to consider the maximum reproductive life span instead of the average reproductive life span in line with Sol et al. (2016) because this variable was available for most of the species

included in our data set (whereas the mean was available only for a smaller subset of highly studied species).

Data Analysis

We built a phylogenetic generalized linear mixed model using Markov chain Monte Carlo (MCMC) analyses with clutch abandonment of either parasitized or unparasitized nests in each study and host species as the response variable. Using a Bayesian approximation as implemented in the R package MCMCglmm (Hadfield, 2010; R Core Team, 2022), we modelled clutch abandonment with a binomial error structure (clutch abandonment was quantified as the proportion of abandoned versus not abandoned clutches, using the 'multinomial2' family in MCMCglmm). We then used a backward stepwise procedure to eliminate nonsignificant effects one by one, starting with the interactions (although single effects involved in significant interactions were kept in the model even if nonsignificant) to obtain the final model.

We included three random effects in our model: (1) 'phylogeny', to account for nonindependence between species due to common ancestry; (2) 'species', as we sometimes had several clutch abandonment data points for the same host species; (3) 'study site', since we sometimes had data for both parasitized and unparasitized nests from the same study site. For the phylogeny, we used the composite topology (Cooney et al., 2017), which combines 'stage 2 Hackett' maximum clade credibility trees from Jetz et al. (2012) with the backbone topology and clade age estimates from Prum et al. (2015), and pruned the tree only to include the host species included in our data set (using the function 'drop.tip' in the package 'ape'; Paradis & Schliep, 2019). We included the frequency of clutch abandonment as the response variable and host breeding range (binary variable segregating prairie from nonprairie host species), host breeding habitat (binomial variable: forest or open habitat), life history (brood value) and relative body mass as explanatory variables. We also included parasitism (a variable determining whether the nest was parasitized or not) and its interaction with all other predictors, the interaction between breeding range and habitat, as well as the triple interaction between range, habitat and parasitism as explanatory variables.

Some studies only included a small number of nests, whereas others considered larger sample sizes. To test whether small sample size studies might shape our results, we also ran our model selection after excluding all studies that monitored fewer than 10 nests (i.e. by only including studies with 10 nests or more). In addition, host species might react differently to the different cowbird species included in our analyses. Because of the low number of data points from studies considering either shiny cowbirds (11 points) or bronze cowbirds (9 points), we could not include the brood parasite species as a predictor in our model. Instead, we ran our model selection again after excluding these two species (and thus, only including results from studies considering parasitism by brown-headed cowbirds). Finally, we tested whether considering nest desertion only instead of the combination of nest desertion and egg burial provided qualitatively different results by also running the model selection considering the frequency of nest desertions (instead of clutch abandonment) as the response variable.

We ran each model for 550 001 iterations with a burn-in interval of 50 000 to ensure satisfactory convergence. We sampled 1000 iterations per model (one every 500 iterations) to estimate model parameters. We checked that autocorrelation levels among samples were lower than 0.1 and assessed chain convergence by visually assessing trace plots and running Gelman–Rubin convergence diagnostic on five chains (all models had a potential scale reduction factor below 1.1; we used the 'gelman.diag' function in the 'coda' package; Plummer et al., 2006). Following Hadfield

(2010), we used a poorly informative inverse Wishart prior ($V = 1$, $\nu = 0.002$) for the variances. We reran the model selection using different prior structures, by varying the values of V (0.1, 0.5) and ν (0.1, 0.5, 1) or considering a parameter expanded prior (with $V = 1$, $\nu = 1$, $\alpha.\mu = 0$, $\alpha.V = 100$), but changing the prior had no qualitative effect on the model outputs and interpretation. To interpret significant interaction effects retained in the final model, we used the 'emmeans' function (package 'emmeans'; Lenth, 2024) to obtain estimated marginal means and their 95% HPD (higher posterior density) for each level.

RESULTS

The final model included the interactions between parasitism and both relative host body mass and breeding habitat (Table 1, Fig. 1). In contrast, brood value (Fig. 2), breeding range (prairie/nonprairie) and all other interaction effects did not predict clutch abandonment and were removed from the model (see Supplementary Material for the output of the initial model). Estimated marginal means calculated to interpret these two retained interaction effects (Table 1) show that parasitized nests were more often abandoned (see also Fig. 1a and b) than nonparasitized ones. In addition, parasitism increased clutch abandonment more strongly in the open as compared to forest habitats (Fig. 1a). Finally, although relatively large and small species showed similar clutch abandonment rates in the absence of parasitism, parasitism increased clutch abandonment more substantially in relatively small as compared to relatively large species (Fig. 1b).

We obtained qualitatively similar results when running the same analysis after either excluding data points with fewer than 10 nests, focusing on studies considering the brown-headed cowbird as a brood parasite, or considering nest desertion frequency rather than the frequency of the combination of nest desertion and burial (see Supplementary Material).

DISCUSSION

We demonstrate in this study that parasitism increased clutch abandonment overall, particularly in habitats with more cowbird–host interactions (i.e. open habitats; Fig. 1a). Brood value (Fig. 2) did not predict clutch abandonment, although smaller, more sensitive species were more likely to abandon a parasitized clutch (Fig. 1b).

Clutch Abandonment: An Antiparasitic Strategy?

In our meta-analysis, clutch abandonment was higher in parasitized versus unparasitized nests across *Molothrus* sp. hosts. This

result supports the idea that clutch abandonment is a response to being parasitized, serving as an antiparasitic strategy like egg ejection (Kilner & Langmore, 2011). Our result also aligns with studies on brown-headed cowbirds and cuckoos in which parasitized hosts exhibited clutch abandonment regardless of the nesting stage, with a significantly lower incidence of abandonment in unparasitized nests (Clark & Robertson, 1981; Hosoi & Rothstein, 2000; Rothstein, 1975; Sulc et al., 2019). Clutch abandonment has been proposed as an alternative antiparasitic strategy in small-sized host species that are unable to eject eggs, although it can be more costly than ejection in terms of both time and energy (Guigueno & Sealy, 2010; Hosoi & Rothstein, 2000). Our finding that smaller species are more likely than larger ones to abandon their clutch in response to parasitism is consistent with this hypothesis (Fig. 1b, Supplementary Table S2). In line with this idea, Roncalli et al. (2017) showed that western Bonelli's warblers, *Phylloscopus bonelli*, were more likely to eject small parasitic eggs than large ones and more likely to abandon their nests when parasitized with large eggs. Further work on variation in the frequency of egg ejection in comparison to clutch abandonment as alternative antiparasitic strategies would bring more insights into our understanding of the evolution of these strategies.

Our results suggest that clutch abandonment can serve as a response to parasitism, wherein abandoners increase their fitness and potentially preserve their residual reproductive value by abandoning their current offspring (Grim, 2007; Servodio & Hauber, 2006). However, parasitism is not the only cue for clutch abandonment, as there is evidence that it can be a generalized consequence of several additive stimuli, like predator disturbance and inclement weather (Goguen & Mathews, 1996; Hill & Sealy, 1994; Soler et al., 2015). As such, our meta-analysis adds parasitism to this list of stimuli, and we show that parasitism alone is enough to initiate clutch abandonment (Fig. 1). By incorporating unparasitized nests as controls in our analysis, we were able to dissociate the influence of a successful parasitism event (i.e. the addition of a cowbird egg in the nest). However, we cannot determine whether the increased clutch abandonment of parasitized nests is due to interaction with a cowbird at the nest (Guigueno & Sealy, 2011) or egg puncturing during parasite visits (Nakamura & Cruz, 2000) or directly due to the addition of a parasitic egg (Guigueno & Sealy, 2011). Female cowbirds are known to engage in egg removal or puncturing during nest visits, although this is usually done in association with parasitism (Fiorini et al., 2009; McMaster & Sealy, 1997; Sealy, 1992). Future studies could experimentally test for the relative importance of these two cues, to determine whether host species are abandoning their clutch in response to host–parasite interactions at the nest or to the addition of a parasitic egg. By integrating such information, we can further

Table 1
Best model explaining clutch abandonment rate in birds parasitized or not parasitized by three cowbird species

Explanatory variable	pm	95% CI	Effective sample size	pMCMC
Intercept	−2.268	[−3.031; −1.447]	1001	<0.001
Sensitivity (mass)	−0.076	[−0.724; 0.468]	1001	0.801
Habitat	−0.847	[−1.602; −0.184]	1001	0.0256
Parasitism	1.474	[0.661; 2.322]	1001	<0.001
Sensitivity (mass)*Parasitism	−0.905	[−1.606; −0.249]	1001	0.010
Habitat*Parasitism	1.217	[0.429; 2.020]	1001	0.004
<i>Phylogeny</i>	<i>0.054</i>	<i>[0.0002; 0.229]</i>	<i>1001</i>	
<i>Species</i>	<i>0.066</i>	<i>[0.0003; 0.242]</i>	<i>1001</i>	
<i>Population</i>	<i>0.077</i>	<i>[0.0003; 0.293]</i>	<i>706.4</i>	

The initial model included the effects of parasitism and its interactions with breeding range (prairie/nonprairie), breeding habitat (forest/open habitat), brood value and a variable measuring sensitivity to parasitism (relative host body mass) on clutch abandonment, as well as the interaction between range and habitat and triple interaction between range, habitat and parasitism. We built a PGLMM with the MCMCglmm function and included species, phylogeny and study site as random effects (italicized in the table). We removed nonsignificant effects using a backward stepwise procedure, resulting in the model shown in this table. See text for further details. pm = posterior mean; CI = credible interval.

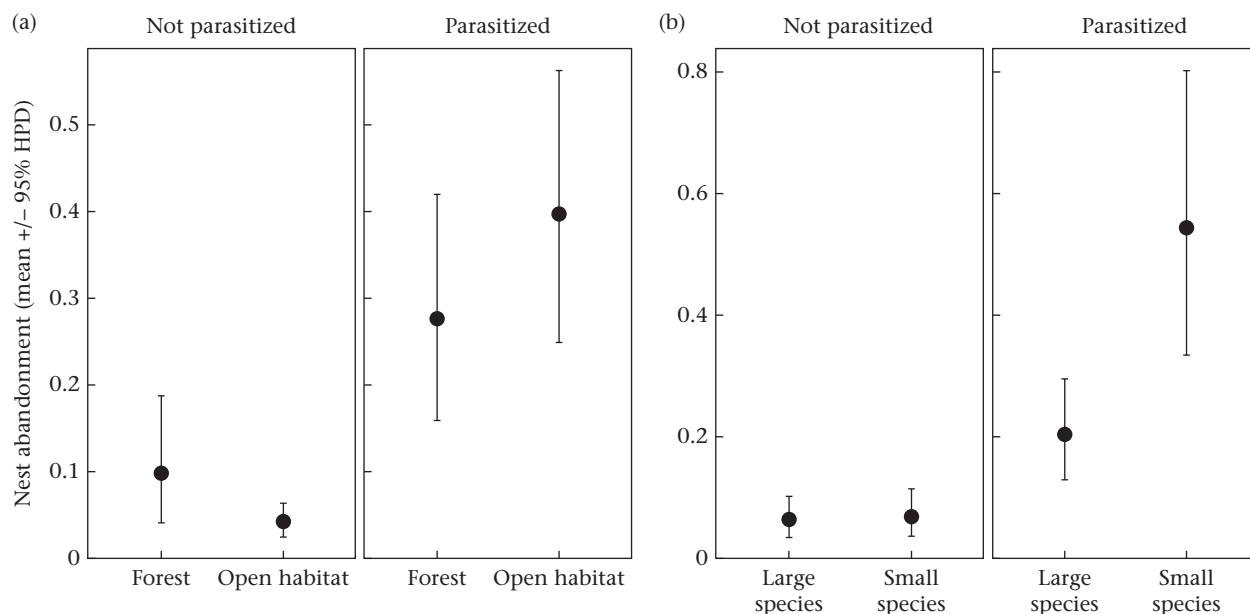


Figure 1. Estimated marginal means for clutch abandonment rates in parasitized and nonparasitized nests (a) in forest and open habitats and (b) in relatively small and relatively large host species. HPD = higher posterior density. The parameters were backtransformed from the log scale and calculated with the ‘emmeans’ function (see main text and Supplementary Table S2).

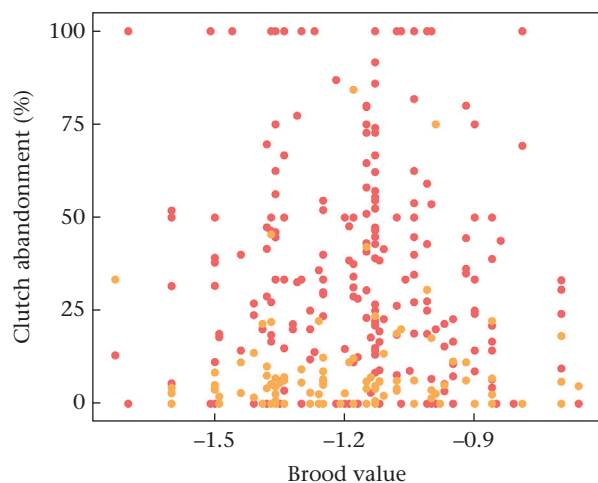


Figure 2. Mean clutch abandonment (%) frequencies of hosts parasitized (red symbols) and not parasitized (yellow symbols) by *Molothrus* cowbirds, relative to their brood value.

elucidate the complex dynamics underlying clutch abandonment behaviours in response to host–parasite interactions.

The Intensity of Host–Parasite Interactions Based on Habitat Predicts Clutch Abandonment

Brood parasitism significantly increased clutch abandonment in open habitats but only had a minor effect in forested habitats (Fig. 1a, Supplementary Table S2). The open habitat/forest difference is likely indicative of a difference in host experience with cowbirds at a small spatial scale: species breeding in forest habitats are expected to encounter cowbirds less frequently, and therefore to be less responsive to them, due to both reduced coevolutionary pressure and individual experience (Blažek et al., 2018; Soler et al., 2012). Hosoi and Rothstein (2000) also found that brown-headed

cowbird hosts in forested habitats were less likely to abandon their parasitized nests than those in open nonforested habitats (see also Mayfield, 1965; Peer & Sealy, 2004). A similar pattern was also detected in cuckoo hosts, where host species nesting in open habitats had more effective rejection defences than forest hosts, interpreted because of their longer exposure to parasitism (Soler, 2014). As forest fragmentation due to agriculture continues to increase, cowbirds are expanding their distribution from forest edges to forest interiors (Robinson et al., 1995; Thompson et al., 2000), which may alter the antiparasitic response of cowbird hosts occupying these fragmented forests. In contrast, breeding range (prairie/nonprairie) did not predict the probability of clutch abandonment in response to parasitism.

Prairie species have historically co-occurred with cowbirds before recent cowbird range expansions (Rothstein, 1994; Smith et al., 2000). Due to this long history, we expected prairie species to be better adapted to respond to parasitism than nonprairie hosts (Hill, 1976; Mayfield, 1965). For instance, grassland hosts are heavily parasitized in the centre of the brown-headed cowbirds’ geographical distribution in the Great Plains (Elliott, 1978; Zimmerman, 1983) and are therefore expected to have evolved stronger antiparasitic responses (Peer & Sealy, 2004; Rothstein, 1975). However, our analyses did not detect such an effect. Instead, more recent and spatially finer-scale interactions with the parasite were a better predictor of the use of clutch abandonment in the context of parasitism.

These results suggest that brood parasite hosts are able to quickly adjust their behavioural response to parasites rather than relying on behaviours inherited from coevolutionary history (but see, e.g. Abernathy et al., 2021), at least with regard to the clutch abandonment strategy. Further work is however needed to better understand the importance of coevolutionary history versus recent exposure to parasites in triggering antiparasitic behaviours, in addition to the importance of learning within a host’s lifetime. Because meta-analyses can sometimes be affected by publication biases (e.g. if studies detecting an increase in nest abandonment in response to parasitism were more likely to be published than studies that failed to detect this pattern), more field studies are

required to investigate these questions in a more causal way. For example, the shiny cowbird, introduced in the West Indies and in South America, offers the opportunity to compare host response to parasitism in its native and introduced ranges, with clear differences in coevolutionary histories. Studies on the evolution of antiparasite behaviour in host species that had never been exposed to this cowbird before its introduction support the idea that recent contact is a strong driver of antiparasitic behaviour evolution (e.g. see Cruz, 1989; Robert & Sorci, 1999).

Clutch Abandonment Varies Independently of Brood Value in Parasitized Clutches

Classic parental investment theory predicts that a parent should increase nest defence intensity with increasing brood value (Trivers, 1972). Because brood value represents the importance of a clutch to lifetime reproductive success, we expected clutch abandonment frequency to decrease with brood value (Bokony et al., 2009). However, brood value did not predict clutch abandonment (Fig. 2). This result was consistent in unparasitized and parasitized nests, suggesting that other parameters are better predictors of clutch abandonment in general and as a response to parasitism. In our analyses, variation in brood value (range -1.73 , -0.66) across host species may be too limited to affect clutch abandonment frequency, since most cowbird hosts are short-lived passerines. The impact of parasitism could also outweigh the importance of brood value in these hosts. However, our finding that the interaction between parasitism and brood value did not significantly predict clutch abandonment frequency suggests that abandonment was not related to brood value, regardless of whether the clutch was parasitized or not. Therefore, overall, brood value was not an important predictor of interspecific variation in clutch abandonment.

Smaller Hosts are More Likely to Abandon Their Parasitized Clutch

Larger species are generally expected to incur smaller fitness costs of parasitism compared to smaller species (Briskie & Sealy, 1990). Consequently, we expected that clutch abandonment in response to cowbird parasitism would be more common in smaller species. In line with this expectation and with results from Hosoi and Rothstein (2000) regarding brown-headed cowbirds, smaller species abandoned their parasitized nests more frequently than larger ones (Fig. 1b). Clutch abandonment is often a common response in small host species that cannot grasp-eject cowbird eggs (Friedmann, 1963; Graham, 1988). This size effect aligns with results from experimental manipulations, finding that medium- and large-sized species desert experimentally parasitized nests at a low frequency compared to smaller species (Lorenzana & Sealy, 2001; Soler, 1990; Underwood et al., 2004; but see Begum et al., 2012). Smaller species may lack the physical ability to selectively remove parasitic eggs from their nests and thus are more likely to use clutch abandonment as an antiparasitic strategy. In addition, the relative cost of raising a parasitic chick to its fledgling size is likely to be higher for smaller as compared to larger host species. Therefore, variations in clutch abandonment frequencies seem to be partly driven by differences in host sensitivity, determined by their respective body size.

Another sensitivity measure not examined in this study is the incubation period. Cowbirds have a short incubation time for their body size, which enables them to hatch earlier than host nestlings (Morrison & Hahn, 2002), providing them with a competitive advantage. This advantage may be particularly pronounced in hosts with longer incubation periods, which may be more sensitive to cowbird parasitism (Briskie & Sealy, 1990). However, there is a

limited range of incubation time variation among small passerines (12.7 ± 0.2 days [95% CI] in our study). Furthermore, the advantage may be mitigated in small hosts with relatively short incubation periods, while relatively large host species could suffer substantially if parasitic eggs hatch well in advance of the host's eggs. Thus, the interaction between body mass and incubation period could influence the extent to which hosts abandon parasitized nests and could serve as an important next step for future research.

Conclusion

Our large-scale meta-analysis covering 85 hosts of the three generalist *Molothrus* species indicates that clutch abandonment, either by nest desertion or egg burial, is triggered by parasitism. As the sensitivity and thus potential cost of parasitism increases (i.e. in small hosts that cannot eject parasitic eggs), so does the frequency of clutch abandonment. Clutch abandonment may allow the host to renest, potentially increasing its lifetime reproductive success. Further studies should help determine whether clutch abandonment in response to brood parasitism is indeed an adaptive strategy.

Data Availability

Analyses reported in this article can be reproduced using the data and code provided in the Supplementary Material.

Declaration of Interest

The authors declare no conflicts of interest.

Author Contributions

Christina Petalas: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Antoine Turcotte-van de Rydt:** Writing – original draft, Methodology, Formal analysis, Conceptualization. **Simon Ducatez:** Writing – review & editing, Writing – original draft, Validation, Software, Methodology, Formal analysis, Conceptualization. **Mélanie F. Guigueno:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2024.06.021>.

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