Look into the Relationships Between Molting, Reproduction, and Parasitism in Birds

Abstract

The relationships between molting, reproduction, and parasitism in birds have all been extensively looked at separately from one another. However, the connection between molting and reproduction are inextricably interlinked to one another due to the well documented energetic trade-off between the two processes. Despite this knowledge, few studies have looked at exactly how these three factors all relate. By comparing the parallels seen in research on molting and parasites, molting and reproduction, and reproduction and parasites, we are able to view a more accurate picture of the energetic trade-offs and other trends relating to wild birds. Since the review is working to connect research on different topics, it is difficult to make conclusions until more extensive studies looking into the interconnectedness between these important three linked factors and the role they play on the fitness of birds.

Expanding Research: Comparing Stressors

As taught in the most basic biology courses, one of the leading stressors leading to natural selection is limitations. There is a finite amount of resources that any organisms with overlapping realized niches must "fight" for in order to survive. Because of the inherent limitations of resources, organisms then have a limited amount of energy to spend on the processes of life. Commonly, it comes down to immune functions, growth, and reproduction.

The goal of every individual to reproduce. In fact, many invertebrates will die right after reproduction. Many different factors affect reproduction, but arguably one of the most important ones is the energetic cost of reproduction. Reproduction is acknowledged as such a serious cost of energy, it has lead to the creation of the "Darwinian demon", a theoretical organism that does not exist with any biological restraints affecting fitness. This hypothetical creature is used in thought experiments to look at evolutionary trade-offs; trade-offs such as growth and immunity (1). Related to the Darwinian demon is the life history theory (LHT). LHT

is how evolutionary ecologists look at how real organisms must manage their resources and limitations in order to maximize fitness: or the ability to successfully reproduce (2).

For birds, another incredibly costly part of life is molting. Molting is the process of birds shedding old feathers and growing new ones. Feather growing is so specialized and well documented that a feather can be pulled and subsequently age, health, and recent reproductive history can all be determined.

An inherent part of parasitism is that the host will have to deal with some degree of cost; in layman's terms, parasites take up energy (3). The virality of the parasite often has a hand in determining the cost to the host; a parasite that is easily passed from vector to vector can have a devastating effect on the host because there is no worry about reproduction/transmission, such as malaria or other common mosquito borne illnesses. But a parasite that needs time to incubate will not kill its host right away. But inevitably, there will still be costs to the hosts; it is these energetic costs (generally used in immunological or behavioral changes) that affect the overall fitness of the individual.

This review will be comparing studies on parasite load, reproduction, and molting. Although there are few papers directly comparing the three, there are many looking at the interaction between two at a time. A wide variety of avian and parasitic species are looked at throughout the review. Though it is generally favorable to focus on one group, maybe a few, the inherent limitations of this topic does require that I reach out beyond some of the normal parameters. The processes of molt and reproduction (and the effect parasitism has on them) are being investigated, and since all birds will go through those two processes as a shared trait within the class *Aves*, the variation amongst the studies does not have a large effect on the review's conclusions.

The Three Stressors

a. Parasites and Molting

To begin, we will be looking at research relating to feather molts and parasites. Surprisingly, both ectoparasites and internal parasites are related to molting, and they had varied effects on feathers. One parasite focused on is one of the most common forms of coccidia found in house sparrows (*Passer domesticus*) is *Isopora lacazei*. Coccidiosis is an infection within the gut lining of a bird. While most birds, and animals, have the parasite oocysts living within their bodies, they tend to not be a problem. But if a bird were to consume too many, too many cells of in their smooth muscles will be destroyed, which can lead to many other issues such as blood poisoning (4). When looking deeper into the effects of the internal parasite, direct negative relationships between primary flight feather regrowth and infection were observed in the house sparrow (5). While primary flight feathers are not only necessary to thermoregulate (and subsequently, decrease metabolic stress) (5) they are also necessary for safety from predation (6). Flight feathers are required to generate thrust and lift and without healthy feathers, the flight can and will be inhibited. Sparrows with internal parasites are shown to have lower feather lengths, vane area, feather mass, rachis width, and barb and barbule density, all of which determine the overall health of the feather (3).

While internal parasites have been often observed have varied effects on external health (7), there are also ectoparasites to consider. Feathers, hair, and fur are all good places for a parasite to hide due to their density. While animals display behavioral efforts (such as different forms of grooming and cleaning) that often will decrease parasite load (7), parasites have been observed to have direct effects on the molts of birds. For a long time, there was a general belief that molting itself was a type of defense against ectoparasites as it appeared to decrease the number of different lice and similar parasites (8). However, when not just examination, but also washings are used there is actually no decrease in feather lice (*Phthiraptera: Ischnocera*) observed after a molt. There only appears to be less because the lice move into the curled pin feathers of feral pigeons (*Columba livia);* such actions provide evidence of coevolution between the two groups as they are able to recognize feathers that will not be shed soon. While mobile

parasites do not decrease, immobile parasites such as fungi or some bacteria *do* decrease, which is logical (3)(9). Interestingly, while there is no true difference between loads of *Bacillus licheniformis* before and after full molts in any bird found carrying the parasite, there *is* a decrease in parasites load during heavy molts (9).

When looking at molting, it is also important to look at the general cost of molting. As previously stated, the fitness of an individual is often determined by how energy is spent. In the case of many birds, it comes down to molting (a form of growth) and how to handle a parasite load. The avian molt itself is an interesting process because it has empirically been proven to be one of the most energetically costly forms of growth measured, including full body molts seen in crustaceans and the ecdysis seen in reptiles (10). The trade-off between immunological functions and molting are handled differently in varying species. When looking at how various birds deal with immune challenges, the great tit (*Parus major*) and the blue tit (*Parus caerulus*) respond by lowering their basal metabolic rates (7). But as established previously, molting requires an increase in metabolic rates to deal with the extra assistance needed for thermoregulation, adding to the already high energetic cost that endothermic species spend (5). Without diving deeply into immunology, another costly form of response, done by the house sparrow, is cell mediation, which is the process of releasing various phagocytes, T-lymphocytes, and cytokines (11); this costs around a 30% increase in energy (7). There have been studies that look directly at the change amount of energy used in molting birds with parasites versus without. When studying body condition, the amount of the hormone corticosterone in feathers (CORTf) and feather condition are both used. When looking at a large group of migratory Arctic birds [northern common eider] (*Somateria mollissima borealis*), upland geese *(Chloephaga picta leucoptera*),and tree swallow (*Tachycineta bicolor*)] infected with avian cholera (*Pasteurella multocida*), there was a stronger relationship between high CORTf levels and low body condition that was not seen in uninfected subjects (12).

(b) Molting and Reproduction

Continuing with the trend of energetic trade-offs, another common energetic trade-off is between growth, or in these scenarios molting, and reproduction. Many different factors of both processes can create major detriments to one another.

Without altering molt directly, changes in the processes surrounding nesting will alter molt -synchronously- further proving their link. When the clutch size of the pied flycatcher *(Ficedula hypoleuca*) was increased, the mother would not start molting until after she was done feeding the fledglings -- no changes from the control were seen when the clutch size was reduced. In the same study, it was also found that hens that delayed their molt had larger and more successful clutches (13). Synchronicity within breeding and molting have an interesting relationship. As shown by the flycatcher, little extra energy is exerted by larger clutches if all eggs hatch at the same time. When molting, there are two different types: synchronous and asynchronous. Many birds molt asynchronously over a period of time ranging from weeks to a year. But diving birds, such as the common eider (*Somateria mollissima*) molt over the period of a few days. This process is highly inefficient because not only do females go into molt right after fledglings leave due to the overlap of food availability (14)(15), each feather takes three percent of the invested to regrow (15).

An important tenet of LHT is that current reproduction will negatively affect future reproductive efforts. To reduce the effects, other energetically demanding processes are usually put off to take place at different times. The speed at which post-nuptial regrowth of primary molts in birds such as European starlings (*Sturnus vulgaris)* is controlled by the decrease in available sunlight, signaling the change in seasons. When male starlings are exposed to artificial changes in exposure, they will then have varied molt/regrowth times. There was a significant decrease in the quality of the primary feathers, the detriments of which have been earlier explained. The decrease in molt time was done to simulant the real world, where breeding, non-

breeding, and late-breeding starlings will have different growth times. The lower quality of feathers is a visible mechanism by which the costs of breeding will affect molts (16).

The established understanding that breeding and molting are both so incredibly demanding is created by the knowledge that molting is almost always delayed until after breeding has finished (16), but both must happen during times with high food availability (14). When looking at 11 different families within the passerine order in South-Central Brazil, there was overlap in molting and brood patches in only 4% of the individual birds, with no correlations among the families. (14).

The relationship between molting times and nesting is not just visible in residential birds. Long-distance migratory birds will often go through a summer molt and winter molt to counteract the energetic costs of breeding, migration, and molting (17). The migratory songbird wood thrush (*Hylocichla mustelina*) goes through partial molts throughout its migration process. Thrushes that nested later were forced to postpone their molts and forced to go through a smaller summer molt and heavier winter molt (18).

(c) Reproduction and Parasites

When looking at reproduction, both ectoparasites internal parasites have visible costs to reproduction. When looking into ectoparasites, they have repeatedly been shown to have negative effects on host reproduction (19)(20). Not only immunological responses have been observed, but as were changes in time-budgeting (which is also a part of LHT) in blue and great tits were infected by the bird flea *Ceratophyllus gallinae*. Significant differences between the behaviors in infected and clean nests were documented. The infected hens were forced to spend extra energy before nesting on cleaning the nest while also sleeping more. However, after hatching, the hens did not show any grooming or nest-cleaning behaviors along with significantly lower times spent sleeping (21). Not only are the behavioral aspects of reproduction affected, but breeding results are as well. When faced with a manipulated seasonal increase in

hen fleas, tree swallows are observed to have a sharp decrease in the quality of the offspring. The health of the hens was monitored using glucocorticoids to show stress, which is also a known reproductive inhibitor. The final conclusion was that parasites are often not the main issue, in combination with a lack of resources or other stressors, then they will exacerbate any other issues (22). There was also the continued trend of visible differences in energy allocations as seen in the tits (21)(22).

An important part of reproductive success goes beyond just successful reproduction: there must also be surviving young. When a nest is infected with parasites, they will move onto the young (23). The tit nests infected by the bird flea lowered the overall health of everyone in the nest; heavily infected hatchlings are born on average 2.1 pounds lighter. By feeding on the hatchlings, the young required more food, which forces the hen to spend more time and energy foraging. However, by day 14 there is no significant difference in the size of hatchlings; meaning that if the hen is able to supplement with more food, the effects the fleas have on the hatchlings can be mitigated at a cost to the hen (21). Blue tits infected with hen fleas see a sharp decrease in the quality and survival of the chicks with a mortality rate 30% higher than uninfected young. The health of the hen was also affected, as they were seen to have significantly decreased body mass than uninfected hens that reproduced at the same time (24). Similarly, a study looking at the American Crow (*Corvus brachyrhynchos)* nestlings infected with three different types of common blood parasites (*Leucocytozoon, Plasmodium,* and *Hemoproteus*) found that early infection of *Plasmodium* lead to high rates of death in fledglings under three years old. While that does not appear significant, 53% of all studied crows were infected with at least one of the parasites (25).

When kittiwakes (*Rissa tridactyl*) are highly infected with a strain of Lyme disease caused by *Borrelia burgdoreri sensu lato*, they will invest less in that clutch than compared to clutches without. A similar pattern is seen in the kittiwakes if they are mating with an “undesirable” mate (26). Such behaviors are indicative that the birds have some concept of the

value of their young; some clutches will be healthier than others, and they will put less effort into the unhealthy clutches. This does differ from the behavior of infected tit hens, who instead put more energy into rearing their infected young. The observed extra effort shown in the blue tit hens is interesting because hens infected with the blood parasite *Haemoproteus* had different approaches to reproduction depending on age. There was a negative relationship between reproductive effort and immunity but only seen in the first year breeders (27). This offers two possible reasonings: either the cost of blood parasites is far higher or that it takes time for the hens to learn to manage parasite load in combination with reproduction.

An Interesting Group: Seabirds

Large seabirds force an interesting perspective when looking at the connection between reproduction and molting due to what could be considered an "odd" cycle compared to the other birds mentioned. There is a well-documented cycle of breeding and molting in many different species of albatrosses, genus *Diomedeidae*, which mate for life in breeding pairs. These large seabirds go through molts that can take up to a year (15). The general observed process is that these pairs do not breed every year in order to leave time to molt. Like most migratory species, there are designated breeding grounds for flocks. Adult albatrosses who were in the breeding grounds did not lose primary feathers. Subadult pairs go through the nesting motions with their mate but do not breed *do* replace worn flight feathers (28). Looking at the relationship between parasite load and molt, while considering known relations between immune costs and the intense cost of replacing feathers, a small study found a correlation between parasite load of the nematode *Seuratia spp*. and recently replaced primaries. Birds with new feather growth had not gone through reproduction recently (28)(29).

Looking at a different group of seabirds, a variety of species (*Bulweria bulwerri, Calonectris diomedea, Puffinus puffinus, P. assimilis baroli, Oceanodrama castro, Larus*

cachinnans atlantis, and *Sterna hirundo*) living in the Azores, similar patterns were found. Like with the albatrosses, all 7 breeds under the review had synchronous cycles between molting and breeding, along with the same trend of molting not occurring on breeding grounds. In 5 of the 7 breeds, there were zero overlaps between molt and breeding times. What little overlap was found was brief and only occurred in fledglings (30).

Concluding Remarks

It is important to note that much of the research used in this review is over 5+ years old. While reviews tend to be written to update new research done, the issue is that new research on this topic is not available because these factors have not been studied at any length, which is why I have been interested in this topic. The field of parasitology is constantly expanding as growing numbers of scientists acknowledge the important role they play as stressors in natural selection and numbers the unique position they hold among trophic levels. As previously shown, plentiful research (though there can *always* be more research) has been done on molting, reproduction, and parasites in every combination but all three. I believe that this is because one of the most important parts of the scientific process is also one of its greatest hindrances: controlled variables. I am a *huge* proponent for controlling as many variables as possible, but it will always hinder the applicability of the research because when not in a laboratory, those controlled variables don't matter anymore.

Possible research directions would be a long-term study monitoring parasite load, molting patterns, and reproductive behaviors on a variety of birds (migratory, passerine, seabirds, etc). Though such research would require intensive tracking, monitoring, and many resources, I believe it would be incredibly beneficial to understanding the greater effects that energetic trade-offs have on the fitness of birds, which has possible applications in agricultural sciences, as well as learning to maintain the health of larger ecosystems.

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Annotated Bibliography

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This paper is an older paper that comes to the conclusion that molting and reproduction is one of the costs of reproduction in birds. Differences in molting time were seen in based on clutch size.

Marini, Miguel Â., and Renata Durães. "Annual Patterns of Molt and Reproductive Activity of Passerines in South-Central Brazil." The Condor 103, no. 4 (2001): 767-75. http://www.jstor.org/stable/1370109.

This study looked over the span of 14 years at the presence of molting feathers (categorized by location of molt) and brood patches. It found that molting generally followed brooding, and that the two processes only overlapped 2% of the time. They also found little-to-no differences between frugivores, insectivores, and omnivores.

Tripet, F., Glaser, M. and Richner, H. (2002), Behavioural responses to ectoparasites: time-budget adjustments and what matters to Blue Tits Parus caeruleus infested by fleas. Ibis, 144: 461-469. doi:10.1046/j.1474-919X.2002.00018.x

This study looks at the blood parasite fleas infesting the nests of brooding blue tits. They changed the flea density of varying nests and studied grooming, egg attendance, nest cleaning, and sleeping during both incubation and nestling.

Péter L. Pap, Csongor I. Vágási, Lőrinc Bărbos, Attila Marton, Chronic coccidian infestation compromises flight feather quality in house sparrows Passer domesticus, Biological Journal of the Linnean Society, Volume 108, Issue 2, February 2013, Pages 414–428, https://doi.org/10.1111/j.1095-8312.2012.02029.x

This paper looks at how coccidian (and comparatively, other internal parasites) affect molting and feather growth over 15 months. It was found that the infected treated birds had significantly poorer quality flight feathers, lighter/shorter primaries, and could potentially decrease the overall fitness of the bird.

Hemborg, Christer, and Arne Lundberg. “Costs of Overlapping Reproduction and Moult in Passerine Birds: an Experiment with the Pied Flycatcher.” Behavioral Ecology and Sociobiology, vol. 43, no. 1, 1998, pp. 19–23., doi:10.1007/s002650050462.

This paper focuses on the other, non-energetic issues with molting and breeding at the same time, such as predation by inducing molt during breeding times. They found that while there was not an effect on female breeding the following year, there was a definite drop in the ability to regrow the primaries during the breeding season.

Richner, Heinz, Anne Oppliger, and Philippe Christe. "Effect of an Ectoparasite on Reproduction in Great Tits." Journal of Animal Ecology 62, no. 4 (1993): 703-10. doi:10.2307/5390.

This study focused on the health and survival of chicks after infestation with the hen flea. While the clutch size and hatching rate was unaffected, the body mass of infested hens was significantly lower. Also, the mortality rates in fledglings varied greatly at 83 vs 53 percent.

Harriman, V.b., et al. “Effects of Ectoparasites on Seasonal Variation in Quality of Nestling Tree Swallows (Tachycineta Bicolor).” Canadian Journal of Zoology, vol. 92, no. 2, 2014, pp. 87–96., doi:10.1139/cjz-2013-0209.

This paper manipulated the number of parasites exposed to a nest before breeding season in order to monitor the glucocorticoids levels of the birds. The research concurred that while parasites are often not the main issue, in combination with a lack of resources or other stressors, then they will exacerbate the issue. There was also the continued trend of visible differences in energy allocations.

Harms N. Jane, Legagneux Pierre, Gilchrist H. Grant, Bêty Joël, Love Oliver P., Forbes Mark R., Bortolotti Gary R. and Soos Catherine Feather corticosterone reveals effect of moulting conditions in the autumn on subsequent reproductive output and survival in an Arctic migratory bird282Proceedings of the Royal Society B: Biological Sciences http://doi.org/10.1098/rspb.2014.2085

This paper also looked at measurable levels of stress through feather corticosterone and the corresponding body conditions of the females. Lower body condition was related to higher levels of CORTf, though no direct connection to CORTf and lay date.

Alex R. Gunderson, Feather-Degrading Bacteria: A New Frontier in Avian and Host-Parasite Research?, The Auk: Ornithological Advances, Volume 125, Issue 4, 1 October 2008, Pages 972–979, https://doi.org/10.1525/auk.2008.91008

This review paper focused on feather-degrading ectoparasites and their effect on birds. While it talked about many other important things that feathers do (that I’m not focusing on), it does talk about molting as a form of parasitic defense. There is found to be fewer parasites during heavy molts, but no change after the molt is completed.

Guillemette, Magella, et al. “Flightlessness And The Energetic Cost Of Wing Molt In A Large Sea Duck.” Ecology, vol. 88, no. 11, 2007, pp. 2936–2945., doi:10.1890/06-1751.1.

This article focuses on the energetic costs, along with the fitness costs, of molting. Increased energy expenditure was measured during molting, along with an increased heart rate. There was proof that solely during the process of asynchronous molt, large amounts of energy were used.

Moyer, Brett R., et al. “Impact of Feather Molt on Ectoparasites: Looks Can Be Deceiving.” Oecologia, vol. 131, no. 2, 2002, pp. 203–210., doi:10.1007/s00442-002-0877-9.

This paper monitored the reduction of lice seen on molting birds versus non-molting birds at the same time, as lots of previous research attributed other stimuli as what decreased parasite load. It found that there is actually not an decrease in mobile parasite load, but instead, the decrease in plummage leads it to appear as if there is a decrease.

Gasparini Julien, McCoy Karen D., Haussy Claudy, Tveraa Torkild and Boulinier Thierry Induced maternal response to the Lyme disease spirochaete Borrelia burgdorferi sensu lato in a colonial seabird, the kittiwake Rissa tridactyla268Proceedings of the Royal Society of London. Series B: Biological Sciences http://doi.org/10.1098/rspb.2000.1411

This study monitors the investment mothers place on clutches based on parasite conditions when laying, similarly to the varying investment known to exist based on the hen’s mate.

Gustafsson L. , Nordling D. , Andersson M. S. , Sheldon B. C. , Qvarnström A. , Hamilton William Donald and Howard Jonathan Charles Infectious diseases, reproductive effort and the cost of reproduction in birds346Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences https://doi.org/10.1098/rstb.1994.0149

This study focuses on the interconnectedness between parasites, nutrition, and reproduction as important mechanisms in the overall fitness of birds. It looked at the antibodies (WBC) in birds related to parasite and reproduction and found a strong correlation between high WBC and low reproductive success.

Marzal, Alfonso, et al. "Malaria Infection and Feather Growth Rate Predict Reproductive Success in House Martins." Oecologia, vol. 171, no. 4, 2012, pp. 853–861., doi:10.1007/s00442-012-2444-3.

This study proved that blood parasites have negative effects on body condition, and subsequently, the ability to regrow feathers. The slowed rate of feather growth was then immediately related to reproduction: negative trends shown in clutch size, fledgling survival, and delayed lay date.

Townsend, AK, Wheeler, SS, Freund, D, Sehgal, RNM, Boyce, WM. Links between blood parasites, blood chemistry, and the survival of nestling American crows. Ecol Evol. 2018; 8: 8779– 8790. https://doi.org/10.1002/ece3.4287

This study focuses on three blood parasites affecting the health of fledglings after parasitization through PCR genetic analysis of blood. Its was found that early fledgling exposure decreased survival rates, though only to some parasites.

Langston, Nancy E., and Sievert Rohwer. "Molt-Breeding Tradeoffs in Albatrosses: Life History Implications for Big Birds." Oikos 76, no. 3 (1996): 498-510. doi:10.2307/3546343.

A study was conducted to look at the molting-breeding pairs in large seabirds, who do not breed every year in order to molt. Adults who entered the breeding colonies did not go through molts, but subadults who go through the nesting motions but do not breed did.

Langston Nancy and Hillgarth Nigella Moult varies with parasites in Laysan Albatrosses261Proceedings of the Royal Society of London. Series B: Biological Sciences http://doi.org/10.1098/rspb.1995.0143

This study looked at caught (already dead) albatrosses, the relation between their most recent molt, parasite load, and most recent reproductive cycle. The study, though it had a very limited sample size and no controlled variables, did see a correlation between replaced primaries and parasite load.

Monteiro, L. R., J. A. Ramos, R. W. Furness, and A. J. Del Nevo. "Movements, Morphology, Breeding, Molt, Diet and Feeding of Seabirds in the Azores." Colonial Waterbirds 19, no. 1 (1996): 82-97. doi:10.2307/1521810.

This paper is a review on the overall life of Azores seabirds, which are different breeds. They all have similar breeding and molting patterns to one another. In 5 of the 7 breeds, there was no overlap in molting and breeding, while in 2 there was only minimal overlap, but only when the young became fledglings.

Dawson A, Hinsley S. A, Ferns P. N, Bonser R. H. C and Eccleston L Rate of moult affects feather quality: a mechanism linking current reproductive effort to future survival267Proceedings of the Royal Society of London. Series B: Biological Sciences

http://doi.org/10.1098/rspb.2000.1254
This study focuses on the quality of quickly grown feathers as proof supporting the life history evolution theory. They manipulated the light the birds were exposed to in order to speed up the process of feather regrowth. They saw that breeding birds will have faster molts (decreasing quality), showing a mechanism by which the cost of reproduction is visible.

Stjernman M. , Råberg L. and Nilsson J. Survival costs of reproduction in the blue tit (Parus caeruleus): a role for blood parasites?271Proceedings of the Royal Society of London. Series B: Biological Sciences ://doi.org/10.1098/rspb.2004.2883
This study was testing the hypothesis that breeding decreases the ability for a bird to fight off parasites as proof of the life history evolution theory. The study showed that in first year breeders, there was a negative relationship between reproduction and parasite resistance.