

Experimental study of social signalling through delayed plumage maturation in a colony-nesting seabird

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Delayed development is a widespread evolutionary strategy that can reduce competition among social animals. Many seabirds exhibit delayed plumage maturation, in which young birds spend years in visually distinct predefinitive plumages before attaining the definitive plumage of adults. Previous work hypothesized that predefinitive plumages may function to reduce aggression towards young seabirds at breeding colonies, an idea known from other lineages of birds as the status signalling hypothesis. We tested this hypothesis with visual stimulus experiments at a breeding colony of American herring gulls, *Larus smithsonianus*. We presented painted models of four different plumage classes (first-cycle predefinitive gull plumage, third-cycle predefinitive gull plumage, definitive gull plumage and a Canada goose, *Branta canadensis*, as a control) and measured the aggressive responses of breeding adults at their nests. Breeding gulls responded with significantly less frequent, lower and slower aggression towards the first-cycle plumage and control stimuli compared to the definitive plumage. There were no significant differences in response towards the third-cycle plumage compared to the definitive plumage. These results provide evidence for a status signalling function of the extensive brown plumage characteristic of first-cycle gulls, which may reduce aggression in foraging flocks, on the wintering ground or during young birds' brief visits to colonies. Given the lack of differences in aggressive responses to third-cycle versus definitive plumage, our data do not settle the issue of why third-cycle gulls, which spend more time at colonies than younger birds, also moult in brown, predefinitive plumages. Future research should investigate how immature seabirds may combine plumage, posture and behaviour to mediate social interactions both on and off the breeding ground.

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One evolutionary consequence of sociality is a delayed developmental form that reduces competition among members of a social group. For example, orang-utans reduce the threat of conflict by suppressing the development of male face flanges (Kralick et al., 2023) while some highly social wrasses delay developing male sexual characteristics until potential competitors are absent (Warner & Swearer, 1991). In birds, several lineages have evolved delayed plumage maturation, in which individuals spend multiple years in distinctive predefinitive plumages before acquiring definitive plumages with adult coloration (Hawkins et al., 2012).

Although there are several different hypotheses for the function of predefinitive plumages, one consistent finding across multiple lineages of bird is that these plumages can act as social signals that reduce aggression towards young birds (Hawkins et al., 2012; Lyon & Montgomerie, 1986).

Research with passerine birds has revealed how predefinitive plumages serve as social signals in diverse social contexts. For example, the predefinitive plumages of male long-tailed manakins, *Chiroxiphia linearis*, a tropical lekking species, help reduce aggression for young males gaining access to courtship display sites and male display partners (McDonald, 1993). In cooperative-breeding groups of red-backed fairy-wrens, *Malurus melanoccephalus*, nonbreeding males in predefinitive plumages are subject to less aggression than males in breeding plumages (Karubian et al.,

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2008). For socially monogamous species with delayed plumage maturation in males (e.g. lazuli buntings, *Passerina amoena*), in females (e.g. tree swallows, *Tachycineta bicolor*) or across sexes (e.g. Hawaii elepaio, *Chasiempis sandwichensis*), predefinitive plumages can reduce aggression for young birds attempting to establish nest sites or territories (Muehter et al., 1997; Stutchbury & Robertson, 1987; VanderWerf & Freed, 2003). These studies suggest that delayed plumage maturation plays a key role in mediating aggression in complex social environments such as display leks, cooperative breeding groups and nesting territories.

Here, we investigate the social signalling function of delayed plumage maturation in seabirds at breeding colonies. Prolonged delayed plumage maturation, lasting 2 years or longer, is present in multiple independent lineages of seabirds including gulls (Charadriiformes: Laridae), albatrosses (Procellariiformes: Diomedidae) and gannets (Suliformes: Sulidae). Many species in these lineages have predefinitive plumages that are distinctly darker or drabber than definitive adult plumages (Grant, 1982; Nelson, 1978; Tickell, 2000). The overall ecology, evolution, development and behavioural properties of delayed plumage maturation in seabirds is not yet clear. Observations and model experiments with least auklets, *Aethia pusilla*, showed that predefinitive plumages have the potential to alter social interactions at breeding colonies, with the lighter plumages of older birds provoking less attention from conspecifics than darker, predefinitive plumages (Jones, 1990). Compared to previous work on plumage in passerines, seabirds thus offer an opportunity to study delayed plumage maturation in a new social context: dense breeding colonies. In addition, delayed plumage maturation in passerines is often sexually dimorphic, with one sex both experiencing heightened risks of social aggression and expressing the predefinitive plumages that mediate those risks, whereas delayed plumage maturation in colony-nesting seabirds is sexually monomorphic.

Behavioural observations have raised a functional hypothesis for delayed plumage maturation in seabirds. In many seabird species, immature birds return to nesting colonies while still in a predefinitive plumage, despite not breeding for multiple additional years (e.g. Nelson, 1966; Pickering, 1989). Young birds in predefinitive plumages also occur alongside adult birds in foraging flocks away from breeding colonies (Wakefield et al., 2019). Accordingly, a functional hypothesis is that predefinitive plumages are status signals that reduce the risk of conflict for young seabirds when they start visiting colonies (Taylor, 2024) or competing in foraging flocks. Alternatively, delayed plumage maturation may be socially neutral (i.e. it may serve no social signalling function) if it is merely the by-product of delayed hormonal expression in young, nonbreeding birds (Schaedler et al., 2021).

We tested the status signalling hypothesis with a model presentation experiment at a breeding colony of American herring gulls, *Larus smithsonianus*. We simulated conspecific birds in different plumage stages near the nests of breeding gulls, using plastic models painted to match different predefinitive and definitive gull plumages, as well as a heterospecific control stimulus. We measured the aggressive responses of breeding gulls to presentations of (1) a young, first-cycle predefinitive gull plumage, (2) an adolescent, third-cycle predefinitive gull plumage, (3) a definitive gull plumage and (4) a Canada goose, *Branta canadensis*, as a control. We predicted that nesting gulls would respond most aggressively to the definitive models and less aggressively to the first-cycle, third-cycle and control models based on the status signalling hypothesis. Alternatively, if predefinitive plumages are socially neutral, we predicted that breeding gulls would respond with equal aggression levels to all gull plumage models. This experiment provides an opportunity to investigate how

predefinitive plumages may function as social signals to mediate aggression at seabird colonies.

METHODS

Study Species and Site

American herring gulls are seabirds that breed in coastal, urban and island colonies across much of northern North America. The species exhibits delayed reproduction and delayed plumage maturation, taking approximately 4 years to begin breeding (as described for the closely related European herring gull, *Larus argentatus*; Chabrzyk & Coulson, 1976) in definitive adult plumage (Grant, 1982).

The definitive plumage in the American herring gull has white body feathers with pale grey wings, black wing tips with white 'mirror' patches, a bright yellow bill and a red gonydeal spot near the tip of the bill (Fig. 1a). Before reaching this definitive plumage, young birds spend approximately 1 year in each of three predefinitive plumage stages: (1) a mottled brown plumage in the first moult cycle, ~12 months old (Fig. 1b); (2) a highly variable, mottled brown plumage with a grey saddle in the second moult cycle, ~24 months old; and (3) a near-definitive plumage featuring grey wings with brown coverts, dark brown primaries, a dark tail band and a yellow bill with merged black and red spots near the tip in the third moult cycle, ~36 months old (Grant, 1982; Nisbet et al., 2017; Taylor, 2024; Fig. 1c).

We conducted our study at the American herring gull breeding colony on Kent Island in the Bay of Fundy, New Brunswick, Canada (44.583°, -66.756°; Fig. 1e). This 80 ha island consists of a large grass field along with patches of spruce and deciduous forest. Up to 6000 gulls breed on the island each year (Bennett et al., 2017). Gulls begin arriving to Kent Island from wintering grounds in the eastern and southeastern United States in the early spring (Anderson et al., 2019; Gross, 1940). They establish nesting territories by early May. The incubation season at the site generally runs from mid-May through mid-June, during which time birds are highly territorial and defend the areas around their nests (Nisbet et al., 2017; Tinbergen, 1953). Both parents assist with incubation, with partners alternating between attending the nest and leaving the territory to forage (Shlepr et al., 2021). Most gulls on Kent Island are breeding birds in definitive plumage, but a small number of first- and second-cycle birds (<1% of the total population) along with a larger number of third-cycle birds (~4% of the total population) are regularly found within the colony as prebreeders (Taylor, 2024).

Primary Visual Stimuli

Our experiment used four visual stimuli as different plumage treatments. Three were plastic gull models (model: SG 1100; Sport Plast Decoy Co., Medelana, Italy). The models were hand-painted with acrylic paint to match different American herring gull plumage stages: first-cycle, third-cycle and definitive (Fig. 1a–c). Because our plastic models were painted with acrylics, they may fail to represent ultraviolet signals visible to at least some seabirds (Capuska et al., 2011), although cryptic ultraviolet patches are unknown in gulls. The control stimulus was a plastic Canada goose (model: AVX-LGCF-4PK; Avian-X Decoys, Irving, TX, U.S.A.), which is a common breeding species on Kent Island that does not regularly exhibit aggressive interactions with gulls (Fig. 1d). There were three exemplars of each gull model and two exemplars of the goose model, for a total of 11 visual stimuli (Supplementary Fig. S1). To minimize the effects of pseudoreplication, exemplars were randomized across trials.

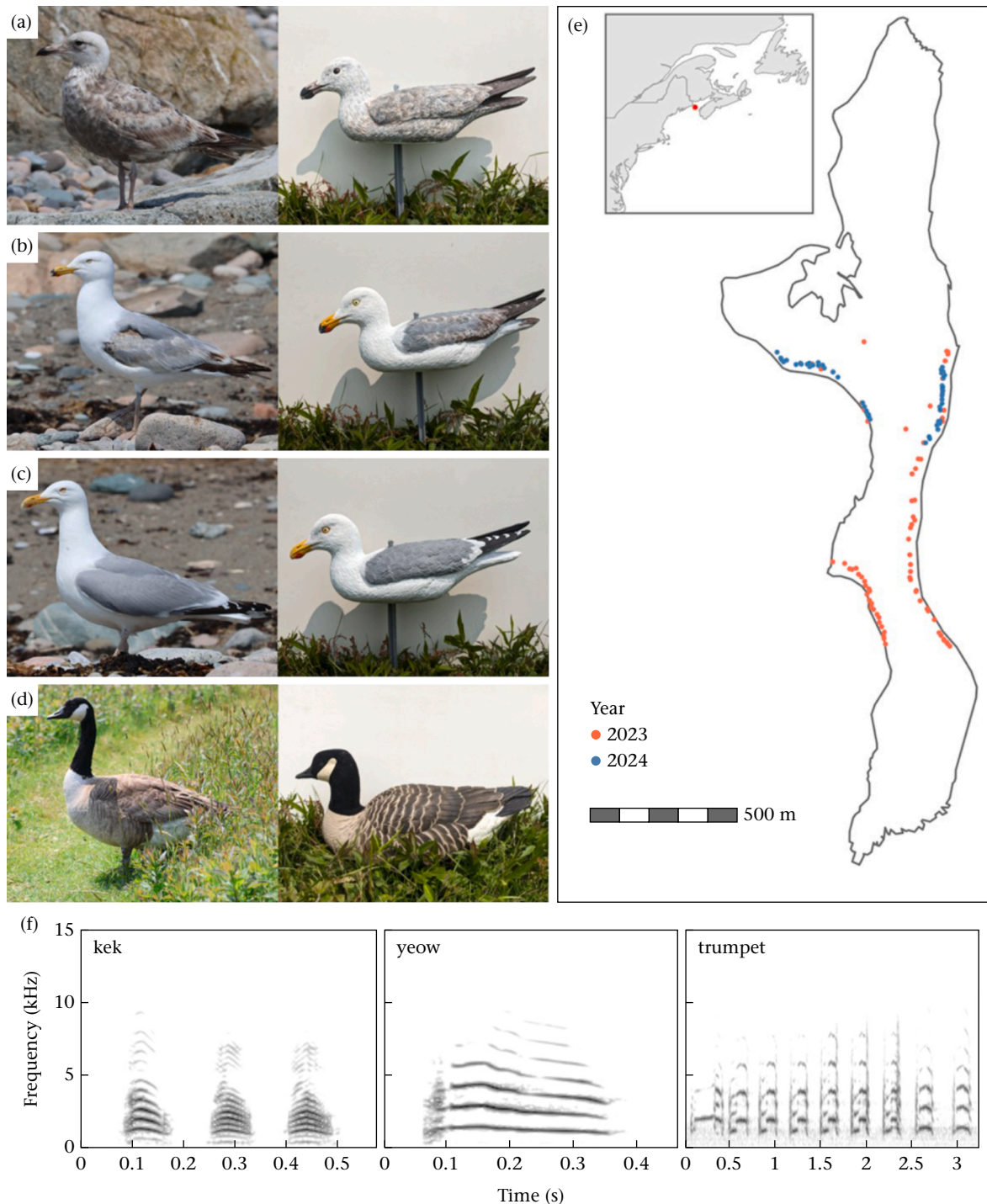


Figure 1. Experimental stimuli and study site for an investigation of plumage signals in American herring gulls. Photographs of (a) first-cycle gull plumage (~12 months old); (b) third-cycle gull plumage (~36 months old); (c) definitive gull plumage (46+ months old); and (d) Canada goose (control), including live birds photographed on Kent Island (left) and photographs of one model of each type (right). (e) A map of the American herring gull breeding colony on Kent Island, New Brunswick, Canada, showing the location of nests used in experimental trials. (f) Sound spectrograms showing an example of each of the calls used in the acoustic stimuli.

Secondary Acoustic Stimuli

We used acoustic stimuli to draw attention to the visual stimuli. Acoustic stimuli consisted of three call types presented in an order corresponding to increasing levels of agitation: 'kek' calls indicating mild alarm, 'yeow' calls indicating moderate alarm and 'trumpet' calls indicating territoriality and social aggression (Nisbet et al., 2017; Tinbergen, 1953). Each acoustic stimulus had

the following structure: 20.0 s of silence; three repetitions of a series of three kek calls, each separated by 3.0 s of silence; 10.0 s of silence; three repetitions of a yeow call, each separated by 3.0 s of silence; 10.0 s of silence; three repetitions of a trumpet call, each separated by 3.0 s of silence (Fig. 1f). We created these stimuli from recordings collected on Kent Island in August 2022. Recordings were collected with an ME62/K6 microphone mounted in a Telinga parabola connected to a Marantz PMD-661 digital recorder (44.1

kHz sampling rate; 16-bit accuracy; WAV format). We selected high signal-to-noise ratio recordings of different individual birds, recorded in different locations throughout the island, producing kek, yeow and trumpet calls.

We prepared playback stimuli using Adobe Audition using three exemplars for each of the three call types. Kek calls are often uttered in a series of three notes spaced closely together (Nisbet et al., 2017). For kek calls, we ensured that each recording had three notes, spaced approximately 0.1 s apart, for a total duration of approximately 0.5 s. For yeow calls, we used individual calls of approximately 0.3 s in duration. For trumpet calls, we used individual calls, each approximately 3.0 s in duration and containing nine notes. We filtered background sounds out of each recording using fast Fourier transform (FFT) filters and the LASSO tool in Audition. We then normalized the amplitude of each recording to -1 dB. We created 27 different audio tracks using all possible combinations of the three recordings of each call type. To minimize pseudoreplication, tracks were randomized across trials. We broadcast audio using a camouflage-coloured JBL Flip 5 speaker. The volume of the loudspeaker was held constant at a level that we determined to be natural in the field based on aural assessment. Later, using a calibrated Casella CEL-24X sound level meter, we measured the amplitude of each call type, and found kek calls were broadcast at 72–76 dB SPL, yeow calls were broadcast at 75–77 dB SPL and trumpet calls were broadcast at 82–86 dB SPL, measured 1.0 m from the loudspeaker.

Nest Selection

We selected nesting territories for each trial in easily accessible field and beach habitat (Fig. 1e), choosing only nests with a parent in attendance. Most selected nests had complete, three-egg clutches (113/120 nests) while the remainder had two eggs. To account for potential variation in parental aggression due to differential investment in the developing clutch (Pierotti & Annett, 1994), we selected only nests that were predicted to be within 1 week of hatching based on egg floatation (Schreiber, 1970). Although some eggs began hatching across the multiple trials that took place at a single nest, no chicks left the nest area during the experimental period.

Experimental Procedure

We tested the aggressive response towards gull plumage signals by presenting models near the subjects' nests, using the four plumage treatments at each nest in a randomized order. Each trial at a nest was separated by 24–36 h to minimize disturbance and habituation effects. With 120 nests and four plumage treatments per nest, the total number of trials was 480.

For each trial, one observer approached the nest with the visual stimulus and the loudspeaker. Models were set upright on a freely spinning, plastic spike ~0.75 m from the nest and the loudspeaker was placed underneath (Supplementary Fig. S2). That observer started the playback stimulus and began briskly walking away from the nest, at which point a second observer started a timer. These two observers helped categorize the behavioural responses of parents along with the time at which each behavioural response first occurred. Territorial and nest defence behaviours can vary when both parents are present at the nest (Shah et al., 2025), so we also recorded the number of parents present at each trial (one, two, or zero if adults left the area at the start of the trial). Because many trials featured only one parent, we did not analyse the sex of these unmarked birds using visual comparisons (the sexes are monochromatic, and although males are larger than females, an observer can only make such a differentiation if both parents are

near one another). There were no cases where parents from neighbouring nests directly interfered with the stimuli. Each trial lasted 2 min, or until a bird made physical contact with the visual stimulus. To prevent destruction of the model, we stopped a trial early and removed the stimulus when a bird made physical contact.

Behavioural Scoring

We categorized behavioural responses into five aggression levels (Table 1). These categories included aggression that may function in both territorial displays and nest defence against potential predators. Level 0 (relaxed) was reserved for gulls that exhibited relaxed behaviours such as preening or incubating. Level 1 (alarm) included agitation or alarm responses (e.g. kek calls, yeow calls, rapid pacing, short fluttering flights). Level 2 (social aggression) included territorial or social conflict displays such as mew calls, trumpet calls and grass-pulling displays directed at the model (Tinbergen, 1953). Level 3 (physical threat) included lunging or swooping at the model without making direct contact. Level 4 (physical attacks) included direct contact with the model.

Each trial was assigned a single aggression score, corresponding to the maximum aggression level observed during that trial. We excluded behavioural responses that were clearly directed towards the observers or towards neighbouring birds, retaining other responses for that trial. We excluded trials where birds flushed at the start of the trial and never returned. After these filters, there was a total of 442 trials retained for analysis: 109 trials for the goose control treatment, 110 trials for first-cycle gull plumage, 113 trials for the third-cycle gull plumage and 110 trials for the definitive gull plumage.

Data Analysis

All analyses were conducted using the 'tidyverse' packages in R version 4.4.1 (R Core Team, 2024; Wickham et al., 2019). First, we used a binomial logistic model to test whether the rate of nonaggressive responses (maximum aggression levels 0–1) versus aggressive responses (maximum aggression levels 2–4) differed by plumage treatment. The model included treatment order (1, 2, 3 or 4) and number of parents present as fixed effects, and nest ID as a random effect (Supplementary Fig. S3). We fitted the model using the 'glmer' function from the 'lme4' package (Bates et al., 2015). The intercept categories were the definitive plumage treatment, treatment order 1 and a single parent in attendance for all models.

To investigate different levels of aggression in more detail, we also fitted an ordinal mixed effects model. The ordinal model allowed us to account for five aggression levels of increasing relative intensity without assigning them precise quantitative values. As in the previous model, we included treatment order and number of parents as fixed effects along with nest ID as a random

Table 1
Behavioural aggression levels used for analysis

Level	Category	Description
0	Relaxed	Incubation; preening; standing; regurgitating; eating
1	Alarm	Pacing; rapidly approaching stimulus; fluttering flight; kek or yeow vocalizations
2	Social aggression	Choking displays; grass-pulling displays; trumpet or mew vocalizations
3	Physical threat	Lunging or swooping at stimulus
4	Physical attack	Contact with stimulus

effect. We fitted the model using the 'clmm' function from the 'ordinal' package (Christensen, 2023).

Finally, we tested for differences in speed of aggressive responses using a linear mixed effects model. The response variable in this model was the minimum time needed to reach the maximum aggression level within each trial. We only included trials where there was an aggressive response (i.e. maximum aggression levels 2–4). In addition to treatment order (fixed effect), number of parents (fixed effect) and nest ID (random effect), this model also included aggression level itself (2, 3 or 4) as a fixed effect. We fitted the model using the 'lme' function from the 'nlme' package (Pinheiro et al., 2024).

Ethical Note

All experimental procedures were approved by the Bowdoin Scientific Station, Bowdoin College (Protocol number 2023-0008) and Yale University (Protocol number 2024-20453). Birds were not captured or handled for this experiment. We designed the experiment to minimize the length of exposure of the animals to signals that could be perceived as aggressive.

RESULTS

Nesting American herring gulls responded with variation in their rate of aggressive response to visual stimuli of different gull plumage stages (Table 2, Fig. 2). Across all plumage treatments, 67.4% of trials resulted in a nonaggressive response (298/442 trials; maximum aggression levels 0–1) while 32.6% of trials resulted in an aggressive response (144/442 trials; maximum aggression levels 2–4). Based on binomial mixed effect model estimates, gulls were 48% less likely to respond aggressively to the first-cycle gull plumage treatment ($P < 0.05$) and 86% less likely to respond aggressively to the goose control ($P < 0.001$) when compared to the definitive gull plumage (Table 2). We found no differences in the rate of aggression towards the third-cycle gull plumage, nor were there effects of treatment order or number of parents present during the trial (Table 2).

Similarly, the ordinal model revealed lower aggression towards the first-cycle gull plumage, along with the goose control, relative to the definitive gull plumage (Table 3, Fig. 3). In terms of the maximum aggression level, across all trials, 21.0% peaked at no aggression (level 0) while 46.4% peaked at alarm response (level 1), 4.5% at social aggression (level 2), 12.2% at physical threat (level 3) and 15.8% at physical attack (level 4; Supplementary Fig. S4). We found no evidence for relationships between aggression level and third-cycle gull plumage, treatment order or number of parents (Table 3, Fig. 3).

When analysing aggressive responses only (i.e. response levels 2 and higher), gulls took significantly longer to reach maximum

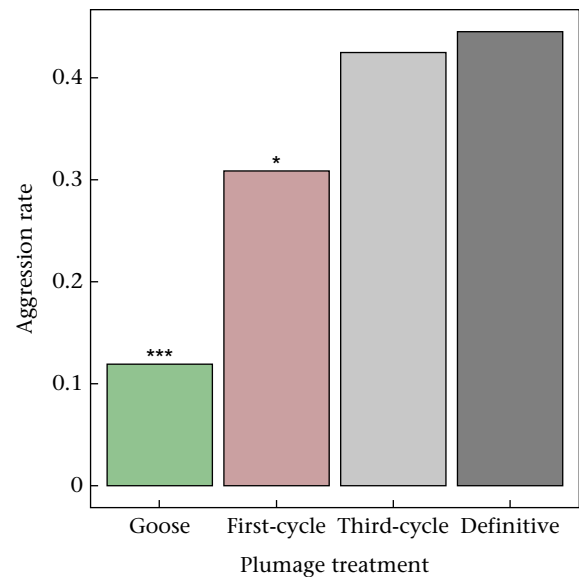


Figure 2. Rate of aggressive responses towards plumage models. Aggression rate was calculated as the proportion of trials reaching a maximum aggression level of 2–4 for each treatment. * $P < 0.05$; *** $P < 0.001$ (compared to the intercept category of definitive plumage, from a binomial mixed effects model).

Table 3

Results of ordinal model for maximum aggression level (0, 1, 2, 3 or 4)

Model term	Estimate	SE	z	P
Plumage – Third-cycle	-0.02	0.26	-0.09	0.93
Plumage – First-cycle	-0.57	0.27	-2.16	0.03
Plumage – Goose	-1.33	0.27	-4.95	<0.001
Trial order – 2	-0.35	0.26	-1.34	0.18
Trial order – 3	-0.41	0.26	-1.58	0.12
Trial order – 4	0.03	0.26	0.13	0.89
No. of parents – 2	0.43	0.26	1.65	0.10

Definitive gull plumage treatment is the intercept category. Significant outcomes are shown in bold.

aggression towards the first-cycle gull plumage (mean $\pm$ SD response time: 43.9 ± 36.1 s) compared to the definitive gull plumage (36.7 ± 27.7 s; Table 4, Fig. 4). We found no evidence for effects on timing from the third-cycle gull plumage (34.9 ± 30.2 s), and a large but statistically insignificant effect from the goose plumage (50.8 ± 37.6 s), although the power of this last comparison was likely limited by the small number of aggressive responses towards the goose.

Aside from plumage, gulls reached peak aggression most slowly in the first trial (47.4 ± 35.2 s), slightly faster in the second (42.8 ± 30.5 s) and much faster at the third (33.4 ± 31.4 s) and fourth trials (34.3 ± 29.1 s; Table 4, Supplementary Fig. S5), with the increases for third and fourth trials being statistically significant. Gulls also responded more slowly when two parents were present (53.2 ± 34.6 s) compared to one parent (36.1 ± 30.2 s; Table 4). Response times did not differ based on level of aggression (Table 4).

DISCUSSION

Multiple orders of seabirds have evolved prolonged delayed plumage maturation (Hawkins et al., 2012), but few studies have investigated the evolutionary significance of predefinitive plumages in these species. Breeding American herring gulls responded towards first-cycle predefinitive plumage stimuli with less frequent aggression (Fig. 2, Table 2), lower aggression levels (Fig. 3,

Table 2

Results of binomial mixed effects model for aggressive response rate

Model term	Estimate	Odds ratio	SE	z	P
(Intercept)	-0.35	0.70	0.30	-1.17	0.24
Plumage – Third-cycle	-0.08	0.92	0.29	-0.28	0.78
Plumage – First-cycle	-0.66	0.52	0.30	-2.20	0.03
Plumage – Goose	-1.96	0.14	0.38	-5.20	<0.001
Trial order – 2	-0.15	0.86	0.32	-0.46	0.65
Trial order – 3	-0.05	0.95	0.33	-0.15	0.88
Trial order – 4	0.46	1.58	0.32	1.45	0.15
No. of parents – 2	0.15	1.16	0.32	0.47	0.64

Trials were considered nonaggressive if they reached maximum aggression levels 0–1 and aggressive if they reached levels 2–4. Definitive gull plumage treatment is the intercept category. Significant outcomes are shown in bold.

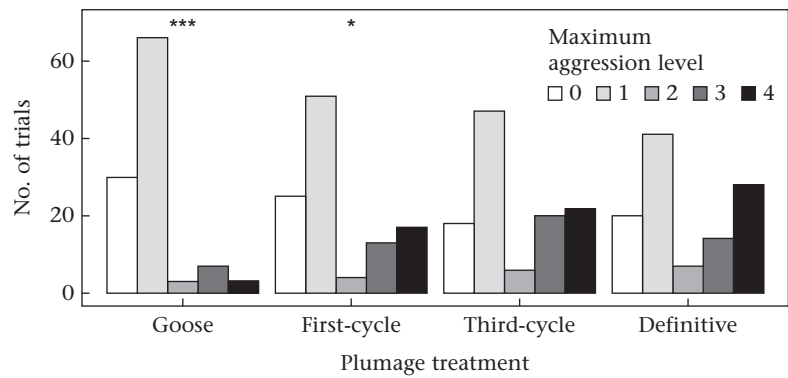


Figure 3. Maximum level of aggression towards plumage models. * $P < 0.05$; *** $P < 0.001$ (compared to the intercept category of definitive plumage, from an ordinal mixed effects model).

Table 4
Results of linear model for time (s) until maximum aggression

Term	Estimate	SE	<i>t</i>	<i>P</i>
(Intercept)	49.22	9.44	5.22	0.00
Plumage – Third-cycle	0.92	6.03	0.15	0.88
Plumage – First-cycle	14.32	6.79	2.11	0.04
Plumage – Goose	18.28	9.87	1.85	0.07
Trial order – 2	-10.29	7.32	-1.41	0.17
Trial order – 3	-16.23	7.20	-2.26	0.03
Trial order – 4	-20.86	7.03	-2.97	0.01
No. of parents – 2	18.15	6.73	2.70	0.01
Max. aggression – 3	-3.50	8.37	-0.42	0.68
Max. aggression – 4	-9.73	8.09	-1.20	0.23

Definitive gull plumage treatment is the intercept category. Significant outcomes are shown in bold.

Table 3) and slower aggressive reaction times (Fig. 4, Table 4) compared to definitive adult plumage stimuli. Our experiment with American herring gulls supports the hypothesis that substantial brown plumage elements, resembling those of first-cycle birds (~12 months old), act as social signals that can reduce the risk of conflict with older, breeding birds (Taylor, 2024).

These results are consistent with previous studies of delayed plumage maturation indicating that predefinitive plumages decrease aggression towards young birds, such as for lekking manakins, cooperatively breeding fairy-wrens and territorial

songbirds (Hawkins et al., 2012; Karubian et al., 2008; Lyon & Montgomerie, 1986; McDonald, 1993; Schaedler et al., 2021; VanderWerf & Freed, 2003). These studies focused on sexually dimorphic species, where female predefinitive plumages generally reduce competition among young males that are beginning to compete for territories or display opportunities. In contrast, delayed plumage maturation in seabirds is sexually monomorphic, with predefinitive plumages that are unique to immature birds rather than resembling a particular sex. This pattern suggests that delayed plumage maturation in seabirds has evolved in line with their social systems, which typically involve social monogamy with biparental territoriality and offspring care (Cockburn, 2006; Lack, 1968). A promising opportunity for future studies of delayed development would involve comparing the dynamics of delayed plumage maturation across sexually dimorphic lineages (e.g. some songbirds or lekking birds) versus sexually monomorphic lineages (e.g. some seabirds or large raptors).

Although we found differences in responses to first-cycle versus definitive plumage stimuli, there is an important discrepancy between our predictions from the status signalling hypothesis and our experimental results. The status signalling hypothesis for seabirds suggests that predefinitive plumages evolved in the context of aggression at breeding colonies, allowing young birds to develop social and territorial skills necessary to begin breeding themselves (Taylor, 2024). Birds of many seabird species return to

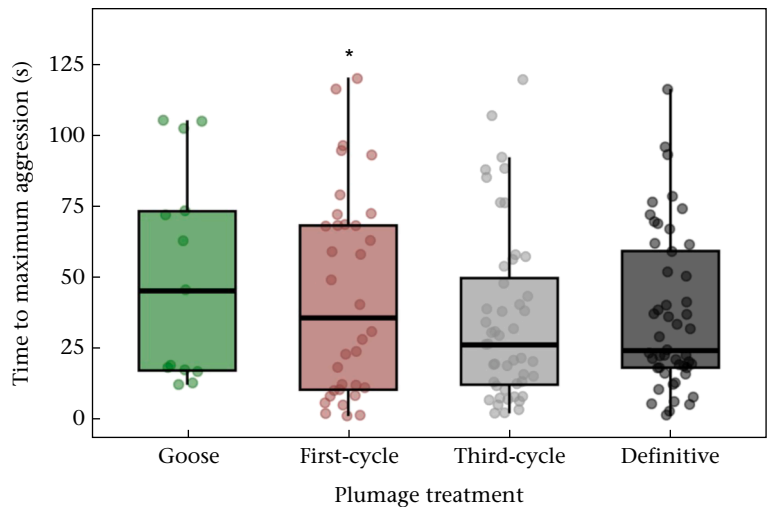


Figure 4. Time to maximum aggression towards plumage models. Only trials with an aggressive response score of 2 or higher were included, limiting the sample size for the goose control. * $P < 0.05$ (compared to the intercept category of definitive plumage, from a linear mixed effects model).

colonies for years before breeding (Nelson, 1978; Pickering, 1989), despite colonies being dense social environments with frequent competition and physical aggression (Coulson, 2002). This hypothesis has been invoked to explain the plumages of third-cycle gulls, which are the most common predefinitive birds at breeding colonies, whereas first-cycle and second-cycle birds are less common (Taylor, 2024). Yet our experiment found no difference in aggression towards the third-cycle plumage treatment compared to the definitive plumage treatment.

One possible explanation for the difference in aggression towards first-cycle versus definitive plumages, but a lack of difference for third-cycle versus definitive plumages, is that gull status signals have evolved in the context of social environments other than the breeding colony itself. Although first-cycle gulls are relatively rare at breeding colonies, they may still experience aggression off the colony at foraging flocks or on the wintering grounds. Intraspecific competition away from the colony can impact both foraging success and spatial segregation for young seabirds (e.g. Fayet et al., 2015; Ulfstrand, 1979). The predefinitive plumages we observe on the breeding grounds may in fact evolve via selection on social dynamics elsewhere (cf. Rohwer & Butcher, 1988). This possibility raises a new link between the social dynamics of seabirds at nonbreeding or foraging grounds and the consequences of those dynamics at the breeding colony.

If gull predefinitive plumages evolved primarily through selection on younger, first-cycle birds at nonbreeding or foraging grounds, then it remains unclear why older, third-cycle gulls still moult in brown, predefinitive plumages. Third-cycle birds may exhibit features that directly mark them as mature competitors, such as a pronounced silver mantle or the red gonydeal spot used as a signal between breeding adults and their hungry chicks (Fig. 1a versus Fig. 1b; Tinbergen, 1953; Tinbergen & Perdeck, 1950). More generally, however, the predefinitive plumages of gulls, like many other seabirds, appear less like discrete categories and more like a gradient across age classes. Third-cycle birds moult in fewer predefinitive plumage elements than second-cycle or first-cycle birds, running all the way down to the fully brown, mottled natal plumages of chicks. This pattern raises the possibility that the status signalling properties of gull predefinitive plumages do not vary discretely across age classes, but rather covary with the amount of brown plumage on display. If so, our experiment may have failed to represent the salient signalling features for third-cycle birds. Much of the brown plumage retained on third-cycle gulls is visible only on the spread wing (Supplementary Fig. S6) and was consequently not visible on our folded-wing models. Furthermore, the placement of these brown plumage patches would suggest that gulls could alter the signalling properties of their plumages through opening their wings or other postural cues.

Posture plays a critical role in gull conflict, including in the display of aggression itself. For example, gulls extend, contract or lower their neck to indicate alarm or aggression during social interactions (MacLean & Bonter, 2013; Stout & Brass, 1969; Tinbergen, 1953). We note that our approach to quantifying aggression, using five broad categories, may have obscured these postural cues and overlooked subtle but important variations in the response of breeding gulls towards different stimuli.

The relationships between physical appearance, posture and behaviour are difficult to disentangle. Indeed, these relationships have confounded our understanding of delayed plumage maturation in seabirds. Previous observers noted that young gulls with brown plumages are attacked more frequently by breeding adults, not less (Huntington, 1954; Taylor, 2024; Ulfstrand, 1979). However, they were unable to distinguish the effects of plumage and behaviour using observational methods alone. Following classic

work on visual signalling (Jones, 1990; Tinbergen & Perdeck, 1950), posture (Galusha & Stout, 1977; Stout & Brass, 1969) and nest defence (Shah et al., 2025), our study suggests that visual stimulus experiments in gulls continue to offer insights into the complicated social lives of seabirds.

Author Contributions

Molly M. Hill: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Sarah L. Dobney:** Writing – review & editing, Methodology, Investigation, Data curation. **Liliane K. Fanburg:** Writing – review & editing, Methodology, Investigation. **Daniel J. Mennill:** Writing – review & editing, Methodology. **Liam U. Taylor:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Data Availability

All data and code for this manuscript are available at Dryad: <https://doi.org/10.5061/dryad.kkwh70sh6>.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2026.123616>.

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