The Journal of Raptor Research - Letters

Pre-definitive plumage in Golden Eagle *Aquila chrysaetos* – an aggression or submission signal?

Jan Ove Gjershaug, Duncan Halley and Bård Gunnar Stokke

Norwegian Institute for Nature Research

P.O. Box 5685 Torgarden, 7485 Trondheim, Norway

Corresponding author: jan.gjershaug@nina.no, phone: +47 46418141

Gjershaug, J.O.; Halley, D.; Stokke, B.G.
Predefinitive Plumage in the Golden Eagle (Aquila chrysaetos): A Signal of Aggression or Submission?. *The Journal of raptor research* 2019 ;Volum 53.(4) s. 431-435
10.3356/0892-1016-53.4.431

In most species of birds, immature plumages are more cryptic than later plumages (Bostwick 2016). Possible explanations for this include as a means of avoiding predation, and as causing more efficient thermoregulation (Kilner 2006). Alternatively, the submission hypothesis posits that immature plumage can signal lower competitive ability to avoid heightened aggression from adults (Lyon and Montgomerie 1986, Muehter et al. 1997, Vander Werf and Freed 2003).

Young Golden Eagles (*Aquila chrysaetos*) (i.e. 1st winter to 4th winter) have conspicuous white coloration on the basal half of the tail and white patches on the base of the inner primaries and secondaries (i.e. pre-definitive plumage; Bloom and Clark 2001, Liguori 2004, Clark and Pyle 2015). These areas of white are lacking in adults, making it easy to separate young and adult eagles. It is also possible to separate juveniles (i.e. 1st winter birds) from immatures (i.e. 2nd winter to 4th winter birds), even though the general coloration and patching between these age classes are more subtle. Normally, Golden Eagles develop adult plumage after 5-7 years (Forsman 2016). Young Golden Eagles look very different from other young *Aquila* eagles and Golden Eagles are the only member of the genus where young birds have a strikingly more conspicuous plumage than adults. Young Steppe Eagles (*A. nipalensis*) also have patches of white on the wings that are lacking in adults, but young and adult birds are not as strikingly different as in Golden Eagles (Table 1).

According to Negro and Galván (2018), bright feathers worn by adult birds may ease conspecific detection of a displaying individual at a long distance. Accordingly, immature birds should not exhibit bright feathers since they have no territory to defend. Negro and Galván (2018) mention the Golden Eagle as an exception, and state that “without careful

53 behavioural observations and comparative studies, the function of these age-related plumage
54 differences will remain a mystery."

55 Bold dark and white immature plumage has been explained as a signal that allays aggression
56 from territorial adults (Ellis and Lish 2006, Watson 2010, Ellis and Schmitt 2017).
57 Observations made by these authors and many others strongly suggest that intruding
58 immature birds are tolerated more than interloping adults, supporting the submission
59 hypothesis.

60 An objection to the submission hypothesis used to explain the contrasting age-related
61 plumages in the Golden Eagle is that cryptic immature plumage, as in most other *Aquila*
62 species (Table 1), would be enough to signal their lower competitive ability to adult birds. We
63 therefore propose an additional selection pressure for the evolution of distinct immature
64 plumage in Golden Eagles, termed the aggression hypothesis.

65 Inexperienced young Golden Eagles may have difficulties hunting live prey during harsh
66 winter conditions in the Northern Hemisphere. Hence, access to ungulate carcasses may be
67 their only chance of surviving. Immature Golden Eagles have longer secondary remiges, and
68 especially for females, also lower wing loading than adults (Lish et al. 2016). This makes
69 soaring flight more efficient at the expense of the manoeuvrability necessary to capture agile
70 live prey such as the grouse, hares, and marmots which dominate the adult diet in most
71 regions (Watson 2000). It appears probable that this is an adaptation for more favourable
72 energetics while searching for carcasses. We propose that the contrasting dark and white
73 immature plumage in this species has evolved primarily as an aggressive rather than a
74 submissive signal, used to obtain access to the carcasses that they depend on. While on
75 carcasses, young eagles often spread their wings and tail (i.e. mantling) or raise their wings to

76 expose the white tail and wing patches (Fig. 1). Display of this conspicuous plumage may
77 function to advertise that they are willing to fight for a carcass. This benefits them by saving
78 them from attacks from adult birds, preventing unnecessary energy loss and possible injury by
79 avoiding physical confrontations. Older and more experienced birds, less dependent on
80 carcasses, are benefited by recognising this and either waiting for access to the carcass after
81 the immature has fed, or opting to hunt live prey. They also benefit from a clear signal,
82 through avoiding energy demanding and potentially dangerous fights. It was reported in the
83 18th century that young Golden Eagles dominated other eagles at carcasses (Strøm 1762).
84 These eagles were named "skjorvinge" in Norwegian (English; "magpie wing") because of
85 the black and white wing pattern. These were thought to be a different species than the adults
86 (Strøm 1762). Here we set out to examine the aggression hypothesis using observations and
87 data collected previously.

88 Halley and Gjershaug (1998) found that younger Golden Eagles tend to dominate older
89 conspecifics at carcasses during the winter (15 of 21 conflicts, One-sample Binomial Test, n =
90 21, P = 0.08). We reanalysed all observed conflicts from that study, including those between
91 the same birds and therefore not statistically independent.

92 Juveniles (1st winter) attacked immatures (2nd winter to 4th winter) in 17 cases, while
93 immatures attacked juveniles in 14 cases, which is not significantly different statistically
94 (One-sample Binomial Test, n = 31, P = 0.72). Comparing juveniles and immatures, and
95 focusing on defenders, juveniles won in four out of 6 cases (One-sample Binomial Test, n = 6,
96 P = 0.69). Comparing juveniles and immatures, and focusing on attackers, juveniles won in
97 15 out of 25 cases (One-sample Binomial Test, n = 25, P = 0.42). These results indicate that
98 there were no differences in the initiation and outcome of aggression events between juveniles
99 and immatures. The plumage of both age categories (juveniles and immatures) was very

100 similar and presumably had the same function. Therefore, we merged these two groups in
101 comparisons of interactions with adults.

102 Adult Golden Eagles were observed at carcasses 35 times. In seven of these cases they were
103 observed together with a young bird, resulting in conflicts. In two of these, adults were
104 classified as the attackers, while in the remaining five cases the adults were classified as the
105 defenders. Adults lost the conflict in all 7 cases. This suggests that juveniles/immatures have
106 the upper hand in such conflicts.

107 Out of 82 observations of young Golden Eagles at carcasses, conflicts were observed between
108 different young eagles 48 times, while the remaining 34 cases did not result in any conflict.
109 Adults were involved in antagonistic interactions with younger birds (7 out of 35) less often
110 than young birds with other young birds (48 out of 82, $\chi 2 = 10.89$, $P < 0.001$).

111 Relative hunger of each bird involved in the conflict may influence the results above.
112 Individuals that have been at the carcass for a long time (> 20 min) may lose some of the
113 motivation to defend it as they become satiated. We reanalysed our data to include conflicts
114 where the attacked individual had been present at the carcass: 1) for < 20 min; and, 2) for > 20
115 min. Combining all age classes together, defending individuals won in 13 out of 52 cases. Of
116 these 13 cases, we found no difference based on the time the defender was at the carcass prior
117 to the attack (defender at carcass < 20 min, $n = 7$; defender at carcass > 20 min, $n = 6$; One-
118 sample Binomial Test, $n = 13$, $P = 1.00$). In the remaining 39 cases, the attacker won. Again,
119 we found no difference based on the time the defender was at the carcass prior to the attack
120 (defender at carcass < 20 min, $n = 25$; defender at carcass > 20 min, $n = 14$; One-sample
121 Binomial Test, $n = 39$, $P = 0.11$). Thus, it appears that hunger of the defending individual (as
122 measured by time at carcass before attack) did not seem to influence the outcome of the

interaction. However, while we do not know the details of relative hunger between the attacking and defending bird, these results show that attackers won more often (n = 39) than defenders (n = 13) (One-sample Binomial Test, n = 52, $P < 0.001$). This result may indicate that attackers are relatively more hungry than the defenders, but we cannot rule out the possibility that the high momentum of attackers when approaching the carcass may scare off defending individuals.

Relative size of each bird involved in the conflict may influence the results too. We have very few observations of conflicts where both birds were sexed. In conflicts between juvenile and immature birds where sex was known, the smaller males won 7 out of 16 conflicts (One-sample Binomial Test, n = 16, P = 0.80). In 6 out of 7 conflicts where males won, the male was the attacker. Females won 9 out of 16 conflicts. In 5 out of 9 conflicts where females won, the female was the attacker. Hence, the outcome of conflicts seemed to more dependent on the status (attacker/defender) rather than the size of the bird.

Despite their smaller size, Golden Eagles dominated White-tailed Eagles (*Haliaeetus albicilla*) in direct competition for access to carcasses (44 of 50 conflicts won by Golden Eagles (all ages), $P < 0.001$; Halley and Gjershaug 1998). No White-tailed Eagle were observed to successfully resist an attacking Golden Eagle. On one occasion, a juvenile male Golden Eagle displaced seven White-tailed Eagles from on or near a carcass or the immediate vicinity (Halley and Gjershaug 1998). Fourteen conflicts were recorded between adult Golden Eagles and White-tailed Eagles, of which 11 were won by the Golden Eagle (One-sample Binomial Test, n = 14, P = 0.06). Golden Eagles won 9 out of 9 conflicts where they attacked White-tailed Eagles, while they won two out of 5 conflicts where they were attacked by White-tailed Eagles.

In addition to our observations, the leader of the Norwegian White-tailed Eagle project (A. O. Folkestad) studied Golden Eagles and White-tailed Eagles on carcasses each winter from 1979–1994. One winter he observed a minimum of 20 different juvenile Golden Eagles on and near carcasses simultaneously. While he did not record quantitative data, Folkestad reports that juvenile Golden Eagles dominated older birds in most conflicts for access to carcasses (A. O. Folkestad pers. comm.).

In obligate avian scavengers, such as the new world vultures (Wallace and Temple 1987; Donazar et al. 1999) and old world vultures (Mundy et al. 1992, Bosè and Sarrazin 2007), adult birds normally win interactions with juveniles. Most eagles in the *Aquila* genus are known to feed on carcasses (Table 1), but apart from the Golden Eagle, the Wedge-tailed Eagle (*A. audax*) and the Steppe Eagle seem to be the only *Aquila* eagles where the juveniles are apparently dependent on carcasses. The Wedge-tailed Eagle is social with typically up to 12 (exceptionally 40) young birds at large carcasses (Debus and Kirwan 2018). The Steppe Eagle is also gregarious on migration and during winter, where ≥ 20 can be found in a small area (Brown and Amadon 1968), and > 300 have been counted at a landfill in southern Oman (Knobel 2012). Both these species, unlike Golden Eagles, apparently tolerate conspecifics at carcasses.

Dominance over a spatially concentrated and limited food source by immatures, coupled with distinct plumage patterns and high level of aggression, has also been reported in honeyguides (Indicatoridae). In several species of honeyguides, specialized in feeding on beeswax, immatures are especially aggressive and dominate adults at the food source. Immature Greater Honeyguides (*Indicator indicator*) have a highly distinctive plumage and are absolutely dominant at the beeswax source (Short and Horne 2002).

The juvenile Golden Eagle is the only *Aquila* species that is both dependent on carcasses and that normally does not tolerate other large raptors at the carcasses. At the same time, the juvenile Golden Eagle is also the *Aquila* species with the most conspicuous plumage compared to adult plumage. The contrasting dark and white plumage in juvenile and immature Golden Eagles may therefore be a product of natural selection where young eagles that are best able to advertise their high motivation to gain or retain a carcass receive a competitive advantage. However, this plumage may also function as a signal that allays aggression from territorial adults outside a carcass situation; the two hypotheses are not mutually exclusive. In other *Aquila* species, the juvenile plumage has probably primarily evolved to allay territorial aggression from the adults; but without the function as a warning signal, the juvenile plumage in these species, while different, is not more conspicuous than that of adults.

Ackowledgements

We want to thank Jordan Harrison, Matthew Stuber and one anonymous referee for constructive comments that significantly improved the quality of the manuscript. We also thank Livar Ramvik for use of his photo.

LITERATURE CITED

Bosè, M.A., and F. Sarrazin (2007). Competitive behaviour and feeding rate in a reintroduced population of Griffin Vultures *Gyps fulvus*. Ibis 149:490–501.

190 Bloom, P.H., and W.S. Clark (2001). Molt and sequence of plumages of Golden Eagles and a
191 technique for in-hand ageing. North American Bird Bander 26:97–116.

192 Bostwick, K. (2016). Feathers and plumages. In The Cornell Lab of Ornithology handbook of
193 bird biology. Third edition (I.J. Lovette and J.W. Fitzpatrick, Editors). John Wiley and Sons,
194 New York, USA. pp. 101–147.

195 Brown, L., and D. Amadon (1968). Eagles, hawks and falcons of the World, Volume 2. The
196 Hamlyn Publishing Group, Feltham, Middlesex, UK.

197 Clark, W.S., and P. Pyle (2015). Commentary: A recommendation for standardized age-class
198 plumage terminology for raptors. Journal of Raptor Research 49:513–517.

199 Debus, S., and G.M. Kirwan (2018). Wedge-tailed Eagle (*Aquila audax*). In Handbook of the
200 Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie and E. de Juana,
201 Editors. Lynx Edicions, Barcelona, Spain. https://www.hbw.com/node/53163.

202 Debus, S., G.M. Kirwan, and J.S. Marks (2018). Gurney's Eagle (*Aquila gurneyi*). In
203 Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie
204 and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain.
205 https://www.hbw.com/node/53161.

206 Donazar, J.A., A. Travaini, O. Ceballos, A. Rodriguez, M. Delibes, and F. Hiraldo (1999).
207 Effects of sex-associated competitive asymmetries on foraging group structure and despotic
208 distribution in Andean condors. Behavioral Ecology and Sociobiology 45:55–65.

209 Ellis, D.H., and J.W. Lish (2006). Thinking about feathers: adaptation of golden eagle
210 rectrices. Journal of Raptor Research 40:1–28.

211 Ellis, D., and N.J. Schmitt (2017). Behaviour of the golden eagle. An illustrated ethogram.
212 Hancock House Publishers, Washington, USA.

213 Forsman, D. (2016). Flight identification of raptors of Europe, North Africa and the Middle
214 East. Christopher Helm, London, UK.

215 Halley, D.J., and J.O. Gjershaug (1998). Inter- and intra-specific dominance relationships and
216 feeding behaviour of golden eagles *Aquila chrysaetos* and sea eagles *Haliaeetus albicilla* at
217 carcasses. Ibis 140:295–301.

218 Kemp, A.C., and G.M. Kirwan (2018a). Verreaux's Eagle (*Aquila verreauxii*). In Handbook
219 of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie and E. de
220 Juana, Editors). Lynx Edicions, Barcelona, Spain. https://www.hbw.com/node/53164.

221 Kemp, A.C., and G.M. Kirwan (2018b). Tawny Eagle (*Aquila rapax*). In Handbook of the
222 Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie and E. de Juana,
223 Editors). Lynx Edicions, Barcelona, Spain. https://www.hbw.com/node/53156.

224 Kemp, A.C., and G.M. Kirwan (2018c). Cassin's Hawk-eagle (*Aquila africana*). In Handbook
225 of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie and E. de
226 Juana, Editors). Lynx Edicions, Barcelona, Spain. https://www.hbw.com/node/53174.

227 Kemp, A.C., P. Boesman, and J.S. Marks (2018). African Hawk-eagle (*Aquila spilogaster*). In
228 Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie
229 and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain.
230 https://www.hbw.com/node/53166.

Gjershaug, J.O.; Halley, D.; Stokke, B.G.
Predefinitive Plumage in the Golden Eagle (Aquila chrysaetos): A Signal of Aggression or Submission?. *The Journal of raptor research* 2019 ;Volum 53.(4) s. 431-435
10.3356/0892-1016-53.4.431

231 Kilner, R.M. (2006). Function and evolution of color in young birds. In Bird Coloration.
232 Volume 2. Function and Evolution (G.E. Hill and K.J. McGraw, Editors). Harvard University
233 Press, Cambridge, USA. pp 201–232.

234 Knobel, J. (2012). Eagles of Africa. Game Parks Publishing, Pretoria, South Africa.

235 Liquori, J. (2004). How to age Golden Eagles. Birding 36:278–283.

236 Lish, J.W., R. Domenech, B.E. Bedrosian, D.H. Ellis, and M. Payton (2016). Wing loading in
237 North American Golden Eagles (*Aquila chrysaetos*). Journal of Raptor Research 50:70–75.

238 Meyburg, B.U., P. Boesman, J.S. Marks, and C.J. Sharpe (2018a). Steppe Eagle (*Aquila*
239 *nipalensis*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal,
240 D.A. Christie and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain.
241 https://www.hbw.com/node/53157.

242 Meyburg, B.U., and G.M. Kirwan (2018). Eastern Imperial Eagle (*Aquila heliaca*). In
243 Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D.A. Christie
244 and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain.
245 https://www.hbw.com/node/53159.

246 Meyburg, B.U., and G.M. Kirwan, and E. de Jiana (2018b). Spanish Imperial Eagle (*Aquila*
247 *adalberti*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal,
248 D.A. Christie and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain.
249 https://www.hbw.com/node/53158.

250 Montgomerie, R.D., and B.E. Lyon (1986). Does longevity influence the evolution of delayed
251 plumage maturation in passerine birds? American Naturalist 128:930–936.

252 Miehter, V.R., E. Greene, and L. Ratcliffe (1997). Delayed plumage maturation in Lazuli
253 Buntings: tests of the female mimicry and status signalling hypotheses. Behavioral Ecology
254 and Sociobiology 41:281–290.

255 Mundy, P., D., Buchart, J. Ledger, and S. Piper (1992). The Vultures of Africa. Academic
256 Press, London, UK.

257 Negro, J. J. and Galván, I. (2018). Behavioural Ecology of Raptors. In Birds of Prey. Biology
258 and conservation in the XXI century (J. H. Sarasola and J. J. Negro, Editors). Springer, Cham,
259 Switzerland.

260 Orta, J., G.M. Kirwan, P. Boesman, E.F.J. Garcia, and J.S. Marks (2018a). Golden Eagle
261 (*Aquila chrysaetos*). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J.
262 Sargatal, D.A. Christie and E. de Juana, Editors). Lynx Edicions, Barcelona, Spain.
263 https://www.hbw.com/node/53162.

264 Orta, J., G.M. Kirwan, D.A. Christie, P. Boesman., J.S. Marks, and E.F.J. Garcia (2018b).
265 Bonelli's Eagle (*Aquila fasciata*). In Handbook of the Birds of the World Alive (J. del Hoyo,
266 A. Elliott, J. Sargatal, D.A. Christie and E. de Juana, Editors). Lynx Edicions, Barcelona,
267 Spain. https://www.hbw.com/node/53165.

268 Short, L.L., and J.F.M. Horne (2002). Family Indicatoridae (Honeyguides). In Handbook of
269 birds of the World, Volume 7. Jacamars to Woodpeckers (J. del Hoyo, A. Elliott and J.
270 Sargatal, Editors). Lynx Editions, Barcelona, Spain. pp. 274–295.

271 Strøm, H. (1762). Fysisk og økonomisk beskrivelse over fogderiet Søndmør, beliggende i
272 Bergens stift i Norge. Volume 1 (in Norwegian).

273 Vander Werf, E.A., and L.A. Freed (2003). Elepaio subadult plumages reduce aggression
274 through graded status-signaling, not mimicry. Journal of Field Ornithology 74:406–415.

275 Wallace, M.P., and S. A. Temple (1987). Competitive interactions within and between species
276 in a guild of avian scavengers. Auk 104:290–295.

277 Watson, J. (2000). The golden eagle. Second edition. T and AD Poyser, London, UK.

Gjershaug, J.O.; Halley, D.; Stokke, B.G.
Predefinitive Plumage in the Golden Eagle (Aquila chrysaetos): A Signal of Aggression or Submission?. *The Journal of raptor research* 2019 ;Volum 53.(4) s. 431-435
10.3356/0892-1016-53.4.431

278 Table 1. Juvenile and immature plumage, use of carcasses, and aggression in *Aquila* eagles.

279

Species	Are young birds more cryptic than adults?	Do young birds depend on carcasses?	Do young birds tolerate conspecifics at carcasses?	Do young birds tolerate other eagle species at carcasses?	Source	Comments
Aquila chrysaetos	no	yes	no	no	Orta et al. 2018a	
Aquila nipalensis	no	yes	yes	?	Brown and Amadon 1968, Knobel 2012, Meyburg et al. 2018b	Immatures often feed at carcasses during migration and in winter
Aquila audax	yes	yes	yes	?	Debus and Kirwan 2018	Carcasses mainly important during non-breeding season. Gathers (mainly immatures, typically up to 12, exceptionally 40) at carcasses of large animals, where dominates smaller scavengers
Aquila verrauxi	yes	no	?	?	Kemp and Kirwan 2018a	Rarely feeds on carcasses
Aquila adalberti	yes	no	?	?	Meyburg et al. 2018a	
Aquila rapax	yes	?	?	?	Kemp and Kirwan 2018b	May feed on carcasses
Aquila gurneyi	yes	no	?	?	Debus et al. 2018	Feeding habits poorly known

Gjershaug, J.O.; Halley, D.; Stokke, B.G.
Predefinitive Plumage in the Golden Eagle (Aquila chrysaetos): A Signal of Aggression or Submission?. *The Journal of raptor research* 2019 ;Volum 53.(4) s. 431-435
10.3356/0892-1016-53.4.431

Aquila heliaca	yes	?	?	?	Meyburg and Kirwan 2018	Often feed on carcasses during winter
Aquila africana	yes	no	?	?	Kemp and Kirwan 2018c	Feeding habits poorly known
Aquila fasciata	yes	no	?	?	Orta et al. 2018b	
Aquila spilogaster	yes	no	?	?	Kemp et al. 2018	May feed on carcasses

280

Gjershaug, J.O.; Halley, D.; Stokke, B.G.
Predefinitive Plumage in the Golden Eagle (Aquila chrysaetos): A Signal of Aggression or Submission?. *The Journal of raptor research* 2019 ;Volum 53.(4) s. 431-435
10.3356/0892-1016-53.4.431

281 Figure legends

282

283 Figure 1. A juvenile Golden Eagle mantling over a carcass, while the adult Golden Eagle is
284 waiting. Photo by Livar Ramvik.

Gjershaug, J.O.; Halley, D.; Stokke, B.G.
Predefinitive Plumage in the Golden Eagle (Aquila chrysaetos): A Signal of Aggression or Submission?. *The Journal of raptor research* 2019 ;Volum 53.(4) s. 431-435
10.3356/0892-1016-53.4.431

285

286

287 **Figure 1**

Gjershaug, J.O.; Halley, D.; Stokke, B.G.
Predefinitive Plumage in the Golden Eagle (Aquila chrysaetos): A Signal of Aggression or Submission?. *The Journal of raptor research* 2019 ;Volum 53.(4) s. 431-435
10.3356/0892-1016-53.4.431