spricht — die erstaunliche Tatsache, daß die Entwicklung dieser Schmuckhandlungen in einer unseren Schönheitssinn befriedigenden Richtung zu verlaufen scheint, ist damit noch nicht hinreichend erklärt. Der schmückende Laubenvogel freut sich an seinen Zieraten, er sortiert sie nach der Beschaffenheit und Farbe, er prüft sie und verwirft sie, sobald sie unansehnlich werden, ja er bemalt sogar seine Laube — sind dabei Affekte am Werke, die unserer Freude am Schönen und Geordneten verwandt sind? Wie ist es dann zu erklären, daß diese Verhaltensweisen ins Erbgut der ganzen Population übergehen, wenn nicht durch geschlechtliche Zuchtwahl angeborener Varianten?

Incubation Periods of Birds of Prey

A Historical Review by Margaret M. Nice, Chicago 37, Ill., USA

To my very great benefit Dr. Oskar Heinroth sent me in 1931 a reprint of his classic study on incubation periods published in 1922. From this I learned that birds of prey had very long incubation periods and the oft-repeated errors on this subject in American books and papers distressed me.[1] This past winter I started to trace the sources of these errors through Bergtold (1917) and Burns (1915) to Bendire (1892). These authors stated that smaller species of *Falconiformes* incubated 3 weeks (instead of 4 to 5 as they really do), and larger species 4 weeks (instead of 5, 6 and even 8 weeks), and that *Strigiformes* incubated 3 weeks (instead of 4 to 5). Bendire was the main source of these errors. I can find no earlier American book that gives many incubation periods except Gentry (1876, 1882), and his figures were so fantastic that no one quoted them. Where did Bendire get his periods? He and his correspondents could not have watched nests or his figures would have been different.

Heinroth referred to the excellent work of William Evans. This Scottish naturalist, discouraged by the lack of reliable information on incubation periods in the standard works on British ornithology, decided to investigate. He hatched eggs of 79 species in an incubator, or under hens, pigeons and canaries. In 1891 and 1892 he published his results along with an historical survey of incubation periods given by some 40 authors, starting with Tiedemann in 1814. In his discussion he rejects some of the most glaring errors. It is plain that very little was known up to this time on the incubation periods of the birds of prey (and other birds not easy to check), for almost every author gave far too short periods. Evans himself was able to check only two birds of prey — *Falco tinnunculus* 28 days and *Asio otus* 27 days. In the literature he found adequate figures for 4 of the 17 *Falconiformes* listed — *Hieraëtos fasciatus* 40 days, *Falco peregrinus* 30 days, *Buteo buteo* 31 and *Sarcorhamphus gryphus* 54 days; and for 3 of the 5 *Strigiformes* — *Bubo bubo* 34—36, *Athene noctua* 28, and *Nyctea scandiaca* 32—34 days, the last five records from birds nesting in aviaries.

Evans describes how British authors of the 19th century copied from Naumann (1822—1844), Brehm (1861) and from each other; Naumann was "doubtless the origin of most of the periods given by subsequent authors". It seems probable that Bendire accepted the consensus of opinion and decided that American birds would follow the pattern that appeared to prevail across the Atlantic.

The question now arose: Where did Tiedemann and Naumann get their erroneous incubation periods? Tiedemann referred to Aristotle's saying incubation with domestic fowls lasted longer in winter than in summer; I looked up the "Historia Animalium" and found:

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[1] I accept Heinroth's (1922: 173) definition of Brutdauer — "die Zeit ..., die bei regelrechter, d. h. ungestörter Bebrütung eines frischen Eies bis zum Auskriechen des jungen Vogels verstreicht"

"Der Adler brütet ungefähr dreißig Tage, und auch bei den übrigen großen Vögeln dauert die Brütezeit ebensolange, zum Beispiel bei der Gans und der Trappe; bei denen von mittlerer Größe ungefähr zwanzig Tage, zum Beispiel der Gabelweihe und dem Habicht."[2]

So here were the original short periods for birds of prey. But could it have been possible that these errors had been copied for 2200 years? Or did ornithologists in the 19th century hit upon them independently? ARISTOTLE knew that the domestic fowl usually hatches her eggs in 3 weeks and the domestic goose in about 30 days; he inferred that length of incubation varied with the size of bird and assumed that all middle-sized birds matched the hen, all large birds the goose. As to smaller birds he stated that Turtle Dove and Ring Dove incubate 14 days, which is right for the former, but 2 to 3 days too short for the latter. He said the Raven incubates 20 days and the Peafowl 30 days "or rather more"

I had now jumped 20 centuries and found a beginning of the erroneous periods for birds of prey; the problem was to trace ARISTOTLE's statements from 300 B. C. to 1800 A. D. I discovered that PLINY in the first century A. D., ALBERTUS MAGNUS in the 13th century, GESNER in the 16th and ALDROVANDI in the 17th century, all quoted ARISTOTLE's 30 and 20 day periods for *Falconiformes*. No one suggested incubation periods for birds not specifically mentioned by ARISTOTLE, except that ALBERTUS included the Swan among the large birds that incubate for 30 days and GESNER and ALDROVANDI said the White stork incubate a month. In the 18th century almost all the writers referred to ARISTOTLE and his successors, but hardly any one mentioned incubation periods. BUFFON, however, quotes four periods from ARISTOTLE — Eagle, Bustard, Raven, Peafowl and Ring-Dove.

BECHSTEIN's book (1791) seems to have been the first to supply practically all the birds treated with incubation periods. He was familiar with birds of the garden and aviary, but to most of the others he assigned periods according to Aristotelian principles. He doesn't say perhaps they incubate such and such a time; he says they do. Just as his predecessors and most of his successors have done. He mentioned BUFFON and other 18th century writers, but no one earlier. Some of his incubation periods are: *Aquila chrysaëtos* 30 days, *Accipiter nisus* 21, *Milvus milvus* 21, *Falco peregrinus* 18—21, *Bubo bubo* 21, *Glaucidium passerinum* 15 days. NAUMANN (1796) gave almost the same periods that BECHSTEIN did for these and other species. TIEDEMANN cites BECHSTEIN as one of his authorities, but not NAUMANN; he seems to have followed BECHSTEIN, although not exactly.

The succession is clear from ARISTOTLE to BUFFON. BECHSTEIN and NAUMANN may well have been influenced by the traditional 30 days for Eagles and 20 for Hawks. Both believed that length of incubation depends primarily on size of bird and egg and they arranged all species accordingly, assigning 21 days to large Owls and 14—16 days to small Owls, Shorebirds, Terns and Black-headed Gulls.

ARISTOTLE guessed. His guesses were copied for 2200 years. But a few people have investigated, the most notable being EVANS and HEINROTH.

EVANS made a fine start; British ornithologists soon began to take an interest and published incubation periods based on watching nests in the "Zoologist" and "British Birds". These added up to a body of knowledge that was collected in WITHERBY's "Practical Handbook of British Birds" (1920—1924), where fairly good incubation periods were given for over half the birds of prey. Further observations were stimulated so that the "Handbook of British Birds" (1938—1941) presents reliable incubation periods for the majority of the birds included.

HEINROTH in 1908 published incubation periods for over 80 species, among them 3 birds of prey; these were based on eggs hatched in incubators by himself and others.

[2] The word translated by Habicht is Hierax — "the generic term especially for the smaller hawks and falcon" (THOMPSON 1895).

He also gives some general principles concerning incubation. In 1922 he published the most important contribution ever made to this subject. About 100 incubation periods are given, 13 of *Falconiformes* ranging from 28 to 55 days and 7 of *Strigiformes* ranging from 27 to 36 days. The greatest value of this paper lies in the broad principles discussed. He points out that, although there is some relationship between size of egg and length of incubation, especially within a group, on the whole short incubation periods have evolved in response to dangers, and that birds that nest in protected places as holes in trees or in the ground, and those that have few enemies, usually have long incubation periods. This is true of *Procellariiformes, Falconiformes, Psittaci, Striges.* Those with short incubation periods are *Columbidae, Picidae* (despite their nesting in holes), some *Anseriformes,* most *Gallidae, Passeriformes.* Very long incubation periods, especially with altricial birds, are always to be regarded as somewhat primitive. This fundamental paper was well known in Europe and England, but practically unknown in America.

Ludwig Schuster's excellent journal "Beiträge zur Fortpflanzungsbiologie der Vögel" stimulated accurate life history studies with particular attention paid to birds of prey, a much neglected field in America. "Ornithologische Monatsberichte" published incubation periods of *Falconiformes* determined by Rudolf Kuhk in 1924, 1928, 1929. Niethammer's "Handbuch der deutschen Vogelkunde" (1937—1942) gives reliable incubation data. Groebbels (1937) amassed the world's largest list of incubation periods, treating some 2,000 species; in going through his 5,000 references he rejected most of the worst errors, but included some that had better have been forgotten.

In 1922 Heinroth, after mentioning his paper of 1908, wrote: "Dabei sei bemerkt, daß sich in den älteren Werken, besonders in Naumann, unglaublich falsche Angaben über die Länge der Brutdauer finden, die dann meist ohne Nachprüfung und Urteil auch in die neuesten Auflagen der üblichen Handbücher (Friderich, Arnold, Brehm u. a.) übernommen sind." This is still true, for the Neue Naumann (1905), Brehm (1922—1924) and Friderich (1923) still repeat many bad errors.

In Germany and Great Britain the chief problems concerning length of incubation periods have largely been settled as far as ornithologists are concerned, but in America many bird students are still copying errors dating back to Bendire, to Tiedemann, to Aristotle.

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Was reizt den Trauerfliegenschnäpper *(Muscicapa hypoleuca)* zu füttern?

Von Lars von Haartman

Zoologisches Institut der Universität Helsingfors

Im Hinblick auf die beiden grundlegenden Studien DROSTS[1] über den Trauerfliegenschnäpper fällt es nicht leicht, dem „Geburtstagskind" etwas zu überreichen, das mir nur unvollkommen vorkommt. Die im Titel angedeutete Frage ist aber dermaßen verwickelt, daß sie nicht ohne sehr umfassende Versuchsanordnungen restlos zu beantworten ist. Mein Beitrag ist daher nur als eine erste Orientierung über das Problem zu betrachten.

1. Brutgröße und Fütterungsfrequenz

Untersuchungen von MOREAU,[2] KLUIJVER[3] und GIBB[4] haben gezeigt, daß größere Bruten im Durchschnitt öfters gefüttert werden als kleinere. Ob dennoch das einzelne Junge in einer kleineren Brut mehr Futter bekommt als in einer größeren ist noch umstritten.

Die Korrelation zwischen Brutgröße und Fütterungsfrequenz bestätigt sich beim Trauerfliegenschnäpper durchaus, wie automatische Registrierungen an 35 Nestern gezeigt haben (Verfasser und GRÖNBLOM, unpubliziert). Wird die Brutengröße durch Zusatz von Jungen auf 8, 9 oder 10 erhöht — so hohe Jungenzahlen kommen in Finnland in natürlichen Bruten selten bzw. nie vor[5] —, nimmt die Zahl der Fütterungen fortwährend zu. Jedes Junge in sehr kleinen Bruten (B/1—3) erhält verhältnismäßig öfters Futter als in größeren.

2. Die Fütterungsfrequenz einsamer Weibchen

Die Polygamie des Trauerfliegenschnäppers[6] hat zur Folge, daß nicht selten das ♀ allein die Fürsorge für die Jungen übernehmen muß. Es füttert in diesem Fall ungefähr gleich oft wie ein vollständiges Paar mit derselben Brutgröße. Ähnliche Ergebnisse wurden bei Blau- und Kohlmeise erhalten. Wird das ♂ am Nest weggefangen, steigert das ♀ seine Anstrengungen sofort (unpubliziert).

Der umgekehrte Versuch ist einmal durch einen glücklichen Zufall zustande gekommen. Ein ♂ des Trauerfliegenschnäppers fütterte die Jungen allein. Nach einigen Tagen fing ein ungepaartes ♀ an, trotz leiser Angriffe seitens des ♂, Futter zu bringen. Die tägliche Zahl der Fütterungen blieb aber unverändert; nach der Ankunft der Adoptivmutter fütterte das ♂ viel weniger als früher (unpubliziert).

Das Verhältnis zwischen der Zahl der Jungen und den Leistungen der Eltern unterliegt also keiner starren Regelung. Der Nahrungsbedarf der Jungen steht fest, und danach richtet sich in gewissen Grenzen die Leistung der Eltern. Wenn zwei dabei zusammenarbeiten, braucht jedes nur die halbe Arbeit zu leisten.

[1] DROST, Vogelzug 1936; DROST und SCHILLING, Vogelzug 1940.
[2] Journ. Animal Ecology 1947.
[3] Ardea 1950.
[4] Ibis 1950.
[5] VON HAARTMAN, Acta Zoologica Fennica 1951.
[6] VON HAARTMAN, Vår Fågelvärld 1945 und Behaviour 1951.