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SPECIAL REVIEWS IN ORNITHOLOGY

PARTIAL INCUBATION IN BIRDS: ITS OCCURRENCE, FUNCTION, AND QUANTIFICATION

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Early studies of incubation behavior acknowledged the existence of a less regular form of incubation that can occur from the beginning of egg laying to shortly after clutch completion. It has been variously termed "partial incubation" (Putnam 1949, Seel 1968, Ashkenazie and Safriel 1979), "brooding" (Barth 1955), "intermittent incubation" (Samuel 1971), "irregular incubation" (Beer 1962), or "nonrhythmic incubation" (Morton et al. 1972). This form of incubation has been described from visual observations of adults sitting on the nest less regularly, and from egg temperatures that are lower and more variable than those typically attained after clutch completion (Barth 1955, Brackbill 1958, Kendeigh 1963, Barrett 1980, Morton and Pereyra 1985). We refer to this little-understood behavior as "partial incubation" because it is characterized by a reduced amount of time during egg laying that parents sit on and warm their eggs, compared with the amount and intensity of incubation they provide later in the nesting cycle after the clutch is complete. Partial incubation is a common way for birds to initiate incubation.

The onset of incubation, the moment at which a bird begins to incubate a clutch, is a critical event in the avian nesting cycle because it has important effects on fitness, as noted more than half a century ago by David Lack (1947). Incubation onset can affect hatching success and hatching patterns (Nilsson and Svensson 1993, Wang and Beissinger 2009), nestling growth and development (Slagsvold et al. 1995, Bitton et al. 2006), fledging success (Hébert 1993, Hébert and McNeil 1999), and post-fledging survival and recruitment (Cam et al. 2003). Not only can the onset of incubation affect adult reproductive rates, but it also influences and is influenced by parental body condition and survival (Hanssen et al. 2002). Yet the onset of incubation is rarely described and even less commonly quantified, and methods of determining incubation onset have not been standardized among studies or species.

In this review, we (1) clarify terminology for the onset of incubation, refine the concept of partial incubation, and summarize the prevalence of partial incubation. We then (2) examine the potential functions of partial incubation, (3) map individual-level patterns of partial incubation from previous studies onto a recently developed typology of patterns for the onset of incubation (Wang and Beissinger 2009), and examine intraspecific variability and compare interspecific data with respect to taxonomic and ecological diversity. We also (4) provide a standardized method for determining the individual onset of full incubation, using complete records of nest attendance or incubation from the start of laying to beyond clutch completion. Our goal is to show how data from disparate studies can be used to test hypotheses about the function of partial incubation. Finally, we (5) offer questions that may prove to be fertile areas of research and suggest ways to standardize future data collection and analysis to benefit common research goals.

Terminology for the Onset of Incubation

The terms "incubation" and "nest attendance" have at times been used interchangeably (Table 1). Beer (1964) defined incubation as "the process by which the heat necessary for embryonic development is transferred to an egg after it has been laid" (cited in Drent 1975). Early nest attendance that resembles incubation may not effectively warm eggs because of gradual brood-patch development (Bailey 1952, Beer 1962, Massaro et al. 2006). Beer (1962) noted that

> two things are being talked about and are seldom distinguished: the period during which incubation responses are shown by the parents and the period of *effective incubation* as indicated by the time taken for the development of an embryo. [Emphasis added]

These concepts can be operationally distinguished by techniques that observe, measure, or infer adult behavior at the nest (i.e., "nest attendance") versus those that measure egg temperature (i.e., "effective incubation"). Not only are parental incubation behavior and embryonic development measured using different methods, but the time spent by parents in incubating behavior

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may not completely overlap with the developmental time of the embryo. This is the case for many passerines in which egg temperature stays above the developmental threshold during the female's absences from the nest (Kendeigh 1963, Weathers and Sullivan 1989). Alternatively, time spent by parents on the nest but not in contact with the egg may not contribute to development, but may serve other purposes such as adult thermoregulation (Pendlebury and Bryant 2005) or egg cooling (Grant 1982, Walsberg and Voss-Roberts 1983).

A second conceptual duality, related to the intensity of incubation behavior, is that of "partial" versus "full." Full incubation typically refers to the intensity of nest attendance or incubation achieved around or after clutch completion (whether measured as percentage of daily attentiveness or mean daily egg temperature). Full incubation has been variously named (Table 1) to highlight its differences from partial incubation (i.e., less regular incubation mixed with nest attendance during the laying period). The distinction between full and partial incubation is important, because the factors that affect embryo survival may differ before and after clutch completion. For example, eggs exposed to cold temperatures can survive well for several days if they were recently laid, but not if their embryos are older and well developed (Webb 1987).

A few uncommon examples deserve mention here. Full incubation can occur well before laying is complete (such as in species that hatch asynchronously), but species that hatch asynchronously may still display lower levels of incubation during the early laying period (Grenier and Beissinger 1999). Species with a clutch size of one may also display partial incubation, because a plateau in the daily proportion of time spent in incubation (Massaro et al. 2006) or in mean daily egg temperatures (Barrett 1980) may occur much later than the day of egg laying.

It may often be useful to consider partial incubation behavior separately for day and night, because diurnal and noctural nest attendance or incubation often differ (Wilson and Verbeek 1995, Clotfelter and Yasukawa 1999, Hepp 2004). Diurnal measurements could start and end with the active day, as determined by the behavior of the adult; they could follow a fixed period or be determined by the length of civil twilight. Nocturnal measurements would then simply be the complement of the times circumscribed by diurnal measurements. Some researchers may prefer to use a 24-h period, as would be appropriate for polar-breeding species.

THE PREVALENCE OF PARTIAL INCUBATION

We conducted a literature search using the terms "partial incubation" and "incubation onset" in the Web of Science and in the full text of journals in the Searchable Ornithological Research Archive (SORA). The search resulted in 97 papers with information on the onset of incubation in 103 species—some of which were studied multiple times, to yield a total of 123 incubation onset samples (online Appendix; see Acknowledgments). We used information on onset as presented by the authors' own definitions or calculations, or as judged from data shown in published tables and figures. If partial or

TABLE 1. Terms used to describe partial and full incubation.

Partial	Full	Study	Method used	Outcome measured
Earlier incubation, partial incubation of first eggs lying in the nest	Later incubation	Putnam 1949	Continuous visual observation	Nest attendance
Brooding	Incubation	Barth 1955	Fake-egg temperature	Nest attendance
Irregular incubation	Effective incubation	Beer 1962	Sporadic visual observation	Nest attendance
—	Full incubating behavior	Kendeigh 1963	Real-egg temperature	Incubation
Partial incubation	Sufficient incubation for continuous development of the embryo	Seel 1968	Daily nest checks	Incubation
Intermittent incubation	Continuous	Samuel 1971	Nest checks, visual observation	Nest attendance
Nonrhythmic	—	Morton et al. 1972	Nest checks, visual observation	Nest attendance
Partial incubation	Continuous incubation	Ashkenazie and Safriel 1979	Continuous visual observation	Nest attendance
—	Regular incubation	Barrett 1980	Nest temperature, real-egg surface temperature, fake-egg surface temperature	Nest attendance
Incubation *sensu stricto*, any application of heat to the eggs	Continuous attentiveness, continuous incubation	Haftorn 1981	Continuous visual observation, real-egg temperature	Nest attendance, incubation
Laying-stage nest attendance	—	Loos and Rohwer 2004	Hollow-egg temperature	Nest attendance
Any nest attendance or incubation before the onset of full incubation	The proportion of daily attentiveness or incubation achieved after clutch completion	Present study	NA	NA

full onset was not specified by the author(s), we used the earliest day of any nest attendance or incubation as the onset of partial incubation, and the first day that attentiveness or egg temperature reached approximately the mean level after clutch completion as the onset of full incubation. We also abstracted data on developmental mode, hatching pattern, sample size for the onset of incubation, field and statistical methods, and the egg with which collection of incubation data started (online Appendix).

Partial incubation appears to be common during the laying period. Within studies that examined the onset of full incubation in 103 species, 50 species (48.5%) exhibited partial incubation. Among those species that exhibited partial incubation, a disproportionate number ($\chi^2 = 8.35$, df = 2, $P = 0.015$) initiated partial incubation on the day the first egg was laid (27 species, 54.0%), compared with those that started on the day the second egg was laid (13 species, 26.0%) or later (10 species, 20.0%). Thus, partial incubation is common and often begins with the laying of the first egg.

Methods of data collection influenced whether partial incubation was detected. The percentage of samples that detected partial incubation was greater when data collection began on the day the first egg was laid compared with later in the laying sequence (27.6% vs. 16.3%, $\chi^2 = 3.6$, df = 1, $P = 0.057$), as well as when data collection was continuous (e.g., egg temperature recordings) rather than discontinuous (e.g., nest checks) (29.3% vs. 14.6%, $\chi^2 = 6.0$, df = 1, $P = 0.014$). Seventy-seven percent of samples using both criteria ($n = 20$ of 26) detected partial incubation.

The body of literature on incubation onset is not a random sample. Passerines dominated the data set (67 of 123 samples, 54%), but studies that used continuous data collection were most commonly of precocial species (12 of 27, 44%) (online Appendix). Tropical-zone species were underrepresented compared with temperate-zone species (11.4% vs. 56.1% of 123 samples). However, hatching patterns were generally evenly distributed among synchronous species, asynchronous species, and species that spanned both categories.

POTENTIAL FUNCTIONS OF PARTIAL INCUBATION

Many possible adaptive functions of partial incubation could be accomplished with or without the transfer of heat necessary for embryonic development (Table 2). Adaptive functions of partial incubation that would not require embryo development include increasing adult survival or reducing adult energy expenditure, preventing egg loss, and maintaining egg viability. Partial incubation that induces embryonic development could also accomplish any of these functions, because incubation usually requires nest attendance, although warm ambient temperatures can result in embryonic development in the absence of nest attendance.

Functions that do not require incubation.—Partial incubation may benefit adult survival or condition simply through nest attendance. The nest site may provide better protection from predators (Wiebe and Martin 1998) or a more favorable microclimate than other locations (Amat and Masero 2004, Pendlebury and Bryant 2005, D'Alba et al. 2009). For example, European tits roost in the nest during the laying period without raising eggs to incubation temperatures (Haftorn 1978, 1979, 1981). Partial incubation for this purpose does not require physical contact with the eggs; indeed, some species stand over the eggs in the nest cup (Brackbill 1958, Beer 1962, Haftorn 1978, Allen 1980, Haftorn and Reinertsen 1982).

Nest attendance may also prevent egg loss from predation, nest-site takeover, or brood parasitism. If partial incubation serves these functions, early nest attendance would be predicted in populations with intense competition for nest sites (Beissinger et al. 1998), intraspecific or interspecific brood parasitism (Clotfelter and Yasukawa 1999), or high rates of egg predation in relation to adult mortality (Andersson and Waldeck 2006, Kreisinger and Albrecht 2008, Martin and Briskie 2009).

Functions that may require incubation.—Partial incubation could maintain egg viability (Table 2), which can be preserved by either nest attendance or true incubation. Although surprisingly resistant to environmental exposure, avian eggs can perish under immediate threats of constant wetting, temperatures above 40°C, or temperatures near freezing (Batt and Cornwell 1972, Romanoff and Romanoff 1972). Nest attendance can shelter eggs from precipitation, moisture, or solar rays (Morton and Pereyra 1985) as well as from freezing and lethal heat (Grant 1982, Ward 1990). These functions predict that early nest attendance is performed during environmental extremes or in climates subject to these hazards.

Egg viability declines gradually over time under ambient conditions in a wide range of avian taxa (Arnold et al. 1987, Beissinger et al. 2005, Wang et al. 2011), mainly because of two mechanisms: microbial infection and prolonged exposure to unsuitable ambient temperatures. Conditions that promote microbial growth on eggshells, such as a warm, moist environment, can increase the risk of egg infection by fungi and bacteria (Cook et al. 2003, 2005b). Adult nest attendance can alter the microflora of egg shells (Cook et al. 2005a, b; Shawkey et al. 2009) and may promote the competitive inhibition of pathogens that pose a risk of egg infection (Cook et al. 2005a). Early nest attendance also deposits preen oil onto eggs that may favor beneficial or harmless bacteria (Reneerkens et al. 2002, Shawkey et al. 2009). Incubation that raises egg temperatures can activate lysozyme, an enzyme abundant in albumen that has antimicrobial properties against Gram-positive bacteria (Wellman-Labadie et al. 2008).

Prolonged exposure of eggs to temperatures above physiological zero (24–27°C), the temperature below which no development occurs, but below the optimum for incubation (34–36°C), can cause abnormal embryonic development and hatching failure (Webb 1987, Meijerhof 1992). In these cases, incubation may be required to prevent insult to the embryos. Egg viability can also decrease during prolonged exposures to temperatures below physiological zero (Arnold 1993, Wang et al. 2011), perhaps because of changes in albumen pH and viscosity (Fasenko 2007). In this case, partial incubation could advance the embryo to an early stage of development that is more resistant to fluctuations in ambient temperature (Fasenko 2007). These functions predict that partial incubation should occur when ambient conditions could degrade egg viability during the laying period. However, much of the research on embryonic responses to variations in temperature has been performed on domesticated species, and more in situ studies of wild birds are needed.

Functions that require incubation.—All the above functions (adult survival, prevention of egg loss, and maintenance of egg viability) can also be fulfilled if partial incubation contributes to embryonic development. However, initiating or maintaining embryonic development is energetically costly to adults (Moreno et al. 1991, Wiebe and Martin 2000, Cresswell et al. 2004), creates

TABLE 2. Potential adaptive functions of partial incubation.

True incubation required?	Functions	Who benefits		Demographic effect	Example species
		Adult	Egg		
No	Reduce predation of adults	x		Adult survival	White-tailed Ptarmigan[1]
No	Favorable microclimate in nest	x		Adult survival	Kentish Plover,[2] Great Tit,[3] Common Eider[4]
No	Reduce predation of eggs		x	Egg loss	Common Eider,[5] Mallard[6]
No	Prevent nest-site takeover (intra- and interspecific)		x	Egg loss	Green-rumped Parrotlet[7]
No	Prevent brood parasitism (intra- and interspecific)		x	Egg loss	Red-winged Blackbird[8]
No	Shelter eggs from precipitation		x	Egg viability	Mountain White-crowned Sparrow[9]
No	Shelter eggs from moisture (condensation)		x	Egg viability	Mountain White-crowned Sparrow[9]
No	Shelter eggs from solar rays		x	Egg viability	Mountain White-crowned Sparrow,[9] Black-legged Kittiwake[10]
No	Shelter eggs from heat		x	Egg viability	Black-necked Stilt,[11] American Avocet,[11] Snowy Plover,[11] Killdeer,[11] Gull-billed Tern,[11] Forster's Tern,[11] Black Skimmer,[11] Crowned Lapwing,[12] Black-winged Lapwing[12]
No	Shelter eggs from freezing		x	Egg viability	
No	Shelter eggs from microbial growth and infection		x	Egg viability	Pearly-eyed Thrasher[13,14,15]
Yes	Advance embryonic development	x	x	Reproduction	Green-rumped Parrotlet[16]
Yes	Shorten incubation period	x		Adult condition	Common Eider[17]

References: [1]Wiebe and Martin 1998, [2]Amat and Masero 2004, [3]Pendlebury and Bryant 2005, [4]D'Alba et al. 2009, [5]Andersson and Waldeck 2006, [6]Kreisinger and Albrecht 2008, [7]Beissinger et al. 1998, [8]Clotfelter and Yasukawa 1999, [9]Morton and Pereyra 1985, [10]Barrett 1980, [11]Grant 1982, [12]Ward 1990, [13]Cook et al. 2005a, [14]Cook et al. 2005b, [15]Shawkey et al. 2009, [16]Grenier and Beissinger 1999, [17]Hanssen et al. 2002.

developmental asymmetries (Davies and Cooke 1983, Kennamer et al. 1990), and changes the relative amounts of time spent in the egg-laying, incubation, and nestling phases of the nesting cycle (Stoleson and Beissinger 1995). Thus, costs and benefits may be more complex to unravel when partial incubation initiates embryonic development.

For example, partial incubation in anseriforms and galliforms often initiates embryonic development but does not create hatching asynchrony. Hatch synchronization allows later-laid eggs of precocial species to hatch with the rest of the clutch when incubation starts during the laying period (e.g., Vince 1964, Davies and Cooke 1983, Persson and Andersson 1999). Partial incubation thus shortens the incubation period after clutch completion, which reduces the fasting period for females (Hanssen et al. 2002) at the expense of later-laid eggs that hatch in a smaller and less developed state (Davies and Cooke 1983, Persson and Andersson 1999). Anseriforms that continue to feed during the incubation period may still lose body mass (Tombre and Erikstad 1996), so a shorter incubation period would benefit adult body condition. Partial incubation may also maintain the viability of earlier-laid eggs by initiating embryo development, because waterfowl eggs lose viability under ambient conditions (Arnold et al. 1987, Arnold 1993).

Partial incubation that contributes to embryonic development creates hatching asynchrony while maintaining egg viability and preventing nest-site takeover in the Green-rumped Parrotlet (*Forpus passerinus*; Beissinger et al. 1998, Stoleson and Beissinger 1999). Thus, egg survival and viability immediately benefit from partial incubation, but the survival of early hatched chicks is favored over that of later hatched chicks. It is important to determine whether partial incubation starts embryonic development, in which case the effects of partial incubation can be more complex.

METHODS OF MEASURING PARTIAL INCUBATION

The onset of incubation has been quantified in many ways (Table 3). Whether or not partial incubation is detected is highly dependent on the method of data collection. Inferences about the function of partial incubation are strongest when incubation can be distinguished from nest attendance by the simultaneous use of two data-collection methods that record continuously: real-egg temperature and nest attendance (e.g., Barrett 1980).

The ideal way to measure incubation is to obtain the temperature of a real egg in the nest (Caldwell and Cornwell 1975; Haftorn 1978, 1979, 1981; Burger and Williams 1979; Lill 1979; Zerba and Morton 1983; Haftorn and Reinertsen 1985; Morton and Pereyra 1985). However, real-egg temperatures alone are not ideal for measuring nest attendance. Thermal inertia of the egg can make the exact number, length, and starting or ending times of incubation bouts and recesses difficult to discern during high ambient temperatures (J. M. Wang and W. W. Weathers unpubl. data). Parental nest attendance may be more easily inferred from nest temperatures (Norton 1972, Afton 1980, Wilson and Verbeek 1995,

TABLE 3. Methods used to collect data on the onset of incubation.

Type of onset	Measured outcome	Interval	Method	Device	Advantages	Disadvantages
Partial or full	Incubation	Continuous	Temperature	Real egg[1]	Only way of determining embryonic development	Thermal gradients in egg, thermal inertia makes bout-length determination difficult
	Nest attendance			Fake egg[2]	Low cost, ease of use	Requires calibration with real egg temperatures to infer embryonic development
				Nest[3]	Low cost, ease of use	Require calibration with real egg temperatures to infer embryonic development
			Visual	Observer[4]	Detailed record of behavior	Effort-intensive. Nocturnal data difficult to obtain
				Video-recording[5]	Detailed record of behavior	Nocturnal data difficult to obtain
				Time-lapse photography[6]	Detailed record of behavior	Nocturnal data difficult to obtain
				Closed-circuit television[7]	Detailed record of behavior	Nocturnal data difficult to obtain
			Event-based	Event recorder[8]	Ease of interpretation	No additional behavioral information
				Balance under nest[9]	Ease of interpretation	No additional behavioral information
				Radiotransmitter receiver[10]	Ease of interpretation	No additional behavioral information
				Photo-resistor[11]		Custom made. No additional behavioral information
				Weight-sensitive perch[12]		Custom made. No additional behavioral information
				Radio-isotopes[13]	Can distinguish male, female attendance	Custom made. No additional behavioral information
Full	Incubation	Discontinuous	Temperature	Daily nest checks[14]	Ease of use	Assumes incubation absent before eggs warm, constant after
	Nest attendance		Visual	Short-term observation[15]	Ease of use and flexibility	Depending on coverage of laying period, may assume incubation is binary

[1] Caldwell and Cornwell 1975; Haftorn 1978, 1979, 1981; Burger and Williams 1979; Lill 1979; Zerba and Morton 1983; Haftorn and Reinertsen 1985; Morton and Pereyra 1985; Wang and Weathers 2009.

[2] Barth 1955, Holcomb 1974, Ward 1990, MacCluskie and Sedinger 1999, Persson and Göransson 1999, Manlove and Hepp 2000, Poussart et al. 2000, Hanssen et al. 2002, Hubner et al. 2002, Hepp 2004, Loos and Rohwer 2004.

[3] Norton 1972, Afton 1980, Bortolotti and Wiebe 1993, Wilson and Verbeek 1995, Anderson 1997, Sockman and Schwabl 1998, Wiebe et al. 1998b, Grenier and Beissinger 1999, Sockman et al. 2000, Badyaev et al. 2003, Hartman and Oring 2006, Wang and Beissinger 2009.

[4] Putnam 1949, Brackbill 1958, Brewer 1961, Skutch 1962, Davis et al. 1963, Morton et al. 1972, Jackson 1976, Inglis 1977.

[5] Hawkins 1986, Wang and Weathers 2009.

[6] Ashkenazie and Safriel 1979, Derksen 1977.

[7] Haftorn 1978, 1979.

[8] Simons 1981.

[9] Kennamer et al. 1990, Mallory and Weatherhead 1993, Sockman et al. 2000.

[10] Ringelman et al. 1982.

[11] Stenger Weeden 1966.

[12] Marples and Gurr 1943, Gurr 1954.

[13] Coulson and Wooller 1984.

[14] Hann 1937, Fautin 1941, Mickey 1943, Gibb 1950, Lack and Lack 1951, Evenden 1957, Seel 1968, Howell 1979, Murray et al. 1983, Magrath 1992, Nilsson 1993, Viñuela 1997, Potti 1998, Clotfelter and Yasukawa 1999, Rowe and Weatherhead 2009.

[15] Beer 1962, Maxson and Oring 1980, Lessells and Avery 1989, Hébert and Sealy 1992, Banbura and Zielinski 1995.

Anderson 1997, Sockman and Schwabl 1998, Wiebe et al. 1998b, Grenier and Beissinger 1999, Sockman et al. 2000, Badyaev et al. 2003), from temperatures of artificial eggs placed in nests (Barth 1955, Holcomb 1974, Ward 1990, MacCluskie and Sedinger 1999, Persson and Göransson 1999, Manlove and Hepp 2000, Poussart et al. 2000, Hanssen et al. 2002, Hubner et al. 2002, Hepp 2004, Loos and Rohwer 2004, Lord et al. 2011), or video monitoring of the attendance of adults (Haftorn 1978, 1979; Hawkins 1986; Wang and Weathers 2009). Incubation can then be distinguished from nest attendance by noting when egg temperatures are above physiological zero (e.g., Barrett 1980).

Direct observations of parental behavior at nests can provide continuous records of nest attendance, as well as detailed behavioral information such as egg turning, males feeding incubating females, egg guarding or shading, and incubation shift changes. Continuous observer watches have been performed at single nests (Putnam 1949, Brackbill 1958, Brewer 1961, Skutch 1962, Davis et al. 1963) and simultaneously at multiple nests in an open environment (Inglis 1977, Burger et al. 1978). However, observer-performed watches generally do not provide nocturnal data. This is also true of time-lapse photography (Derksen 1977, Ashkenazie and Safriel 1979), video-recording (Hawkins 1986), and closed-circuit television (Haftorn 1978, 1979) unless the cameras are fitted with infrared lenses (eg., Haftorn and Reinertsen 1982, Wang and Weathers 2009). Recent research indicates that nocturnal nest attendance can be far less regular than is often assumed (Wang and Beissinger 2009).

Event-based data collection records the time that adults enter or exit from the nest, reducing continuous monitoring to binary records of nest attendance. Investigators have used event recorders (Simons 1981), balances under the nest (Kennamer et al. 1990, Bortolotti and Wiebe 1993, Mallory and Weatherhead 1993), radiotransmitter receivers (Ringelman et al. 1982), photo-resistors (Stenger Weeden 1966), weight-sensitive perches (Marples and Gurr 1943, Gurr 1954), and radio-isotope traces (Coulson and Wooller 1984) to record nest attendance for multiple days. These data are potentially the easiest to interpret, but they typically sample nest attendance rather than incubation, which requires that a bird in the nest to be in contact with the eggs.

Sporadic data collection is less ideal for studying early incubation but is nonetheless frequently employed. The most basic method for determining the onset of incubation is by noting whether eggs are warm or cold to the touch during a routine nest check (Hann 1937, Fautin 1941, Mickey 1943, Gibb 1950, Lack and Lack 1951, Evenden 1957, Seel 1968, Howell 1979, Murray et al. 1983, Magrath 1992, Nilsson 1993, Viñuela 1997, Potti 1998, Clotfelter and Yasukawa 1999, Rowe and Weatherhead 2009, Arnold 2011). Most studies using this "once daily" method are concerned with the onset of full incubation. This method assumes that eggs are always unattended before the start of incubation, and that once incubation begins the eggs are maintained at a temperature that is warm to the touch. However, both assumptions have been falsified in studies that monitor the nest continuously from the start of egg laying. Short-term opportunistic or systematic visual observations are another method of sporadic data collection (Beer 1962, Maxson and Oring 1980, Lessells and Avery 1989, Hébert and Sealy 1992, Banbura and Zielinski 1995). Depending on their coverage of the laying period, they can pose the same problems as the "once daily" method for inferring the onset of incubation. Short-term observations are more suited to testing hypotheses applicable to full incubation (Conway and Martin 2000), rather than the development of incubation behavior over multiple days.

Multiple studies on the same species illustrate how the type of data collection influences when partial incubation is detected. An early study of the Great Tit (*Parus major*) reported partial incubation starting with the ninth egg (mean clutch size = 10.94, $n = 112$) using daily nest checks (Gibb 1950), whereas later studies using nest-cup temperatures found incubation starting from the third (Haftorn 1981) to the sixth egg (Haftorn and Reinertsen 1982). In the Mountain White-crowned Sparrow (*Zonotrichia leucophrys oriantha*), partial incubation started with the first egg in a study that combined daily nest checks with extensive visual observation (Morton et al. 1972), as well as when egg temperatures were recorded continuously (Zerba and Morton 1983). Thus, discontinuous data collection may agree with continuous methods if the observation window is sufficiently large.

SURVEY OF PATTERNS OF DIURNAL PARTIAL INCUBATION

We recently reported a wide diversity in developmental trajectories of nest attendance prior to full incubation in five passerines (Wang and Beissinger 2009), with high variation in individual trajectories within a species as well as significant variation in the relative frequencies of trajectory types among species. These individual trajectories were classified into "incubation onset patterns" using a general typology based on qualitative criteria that describe patterns of partial incubation that can be applied to all species (Fig. 1). For instance, an individual bird that started incubating with low constancy (percentage of the day incubated) and slowly increased in constancy with each succeeding day was classified as having a "slow-rise" pattern, whereas a bird that initiated incubation at low constancy and achieved the constancy of full incubation within a few days was classified as having a "rapid-rise" pattern. In both of these patterns, incubation constancy rises monotonically (Fig. 1). We termed the incubation onset patterns that rise non-monotonically "irregular," "pulsed," and "step" (Wang and Beissinger 2009). Additional patterns that did not have an overall rise in constancy were termed "W-shape" and "U-shape" (Fig. 1). These 11 patterns were placed into four groups based on the similarity of their incubation trajectories: rising, irregular rising, not rising, and flat (Fig. 1).

We used this typology to manually assign diurnal, full-incubation-onset patterns from published works on individuals from 7 species ($n = 59$ nests) in addition to the 5 species ($n = 73$ nests) used to derive the typology (Wang and Beissinger 2009) (Table 4). We tested whether patterns of individual onset varied by mode of development, hatching pattern, and taxonomic order. The predictions are straightforward for species in which nest attendance during the laying period is effective incubation. We predicted that precocial species with hatch synchronization (e.g., many anseriforms and galliforms; Vince 1964, Davies and Cooke 1983) would have substantial partial incubation and a slow-rise pattern. On the other hand, precocial species without hatch synchronization would be expected to have rapid-rise incubation patterns that start with the last egg of a clutch, to ensure that all eggs receive the same effective incubation. In keeping with our

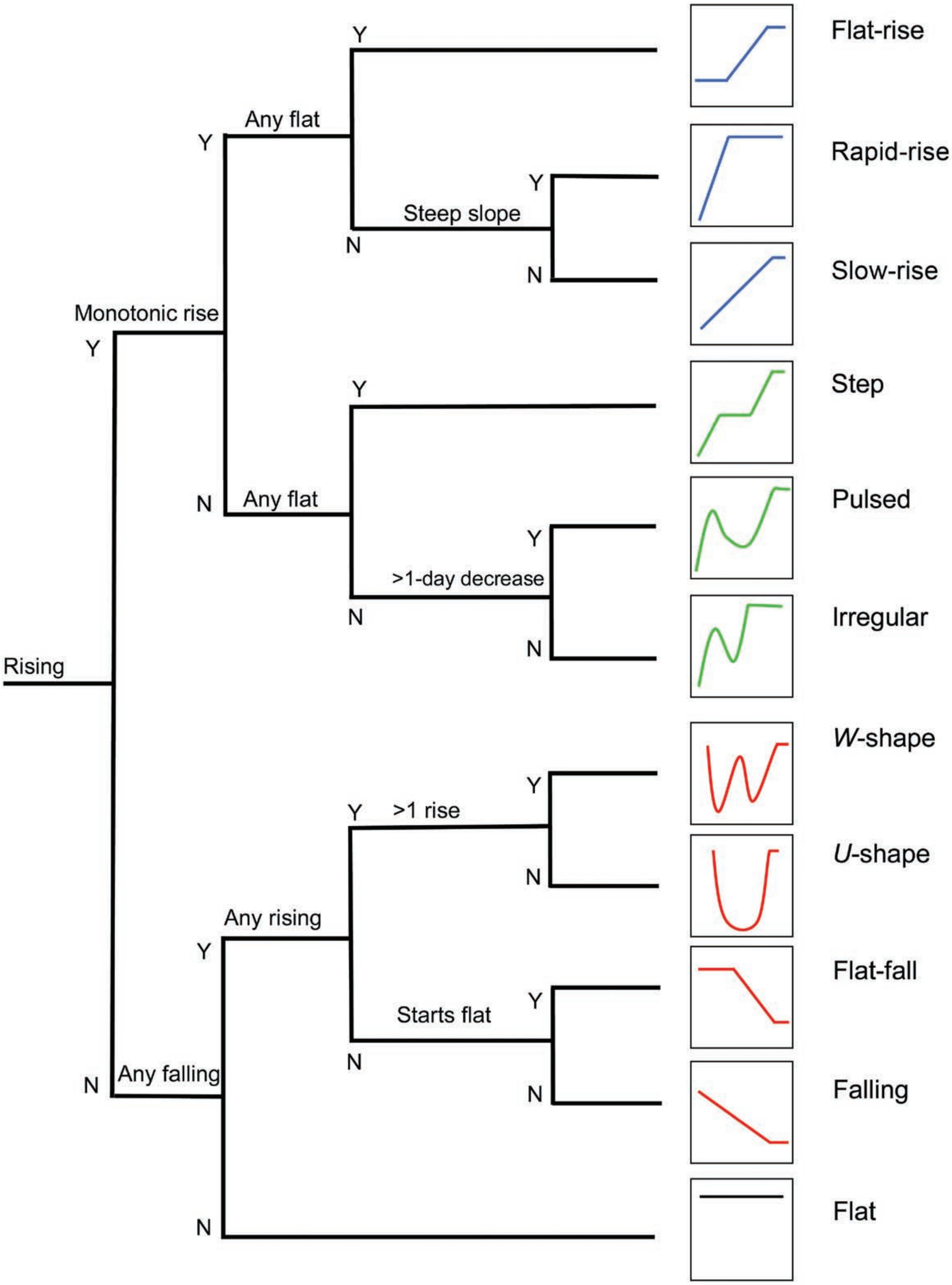

FIG. 1. General patterns for characterizing the onset of full incubation according to whether or not incubation rises monotonically, whether the rise occurs continuously, and the speed and duration of rises. For all patterns, the *x*-axis is days or nights prior to the completion of laying or on the second consecutive day or night after full incubation (whichever came later), and the *y*-axis is the proportion of the day or night incubated. The patterns were categorized into four groups based on similarity: rising (flat-rise, rapid-rise, slow-rise), irregular rising (step, pulsed, irregular), not rising (*W*-shape, *U*-shape, flat-fall, falling), and flat (flat). The data examined for each nest started with the last day or night having ≤1 h of incubation (all flat sections shown are nonzero proportions). The irregular and pulsed patterns could have one or more decreases in incubation. Modified from Wang and Beissinger (2009).

Table 4. Intraspecific variation in full diurnal incubation-onset patterns. Numbers and percentages of individuals in each study are presented. Sample size (*n*) is given for each species for which data were available (total $n = 132$). The outcome measured by each study is shown as either nest attendance (n.a.) or incubation (inc.).

					Rising			Irregular rising			Not rising		
Mode of development	Hatching pattern	Order	Species	Measured outcome	Flat-rise	Rapid-rise	Slow-rise	Step	Pulsed	Irregular	*W*-shape	*U*-shape	*n*
Altricial	Asynchronous	Psittaciformes	Green-rumped Parrotlet[1]	n.a.		3 (25%)	6 (50%)			2 (17%)	1 (8.3%)		12
	Variable	Passeriformes	Ash-throated Flycatcher[2]	n.a.		1 (13%)	6 (75%)			1 (13%)			8
			White-crowned Sparrow[3]	inc.			5 (100%)						5
			Oak Titmouse[2]	n.a.	5 (42%)	2 (17%)	1 (8.3%)		2 (17%)			2 (17%)	12
			Tree Swallow[2]	n.a.	4 (24%)		4 (24%)	6 (35%)		3 (18%)			17
			Violet-green Swallow[2]	n.a.		1 (10%)	5 (50%)	2 (20%)		2 (20%)			10
			Western Bluebird[2]	n.a.	9 (35%)	5 (19%)	8 (31%)	2 (8.0%)	1 (3.8%)	1 (3.8%)			26
			Western Bluebird[4]	inc.	1 (17%)		2 (33%)	1 (17%)		1 (17%)		1 (17%)	6
Semi-altricial	Asynchronous	Falconiformes	American Kestrel[5]	n.a.		2 (50%)	1 (25%)			1 (25%)			4
			Eurasian Kestrel[6]	n.a.	7 (41%)	4 (24%)	2 (12%)	4 (24%)					17
					in rising group								
Precocial	Synchronous	Anseriformes	Northern Shoveler[7]	n.a.			4 (100%)						4
			Snow Goose[8]	n.a.			7 (100%)						7
		Charadriiformes	Semipalmated Sandpiper[9]	n.a.		4 (100%)							4

[1] Grenier and Beissinger 1999. [2] Wang and Beissinger 2009. [3] Zerba and Morton 1983. [4] Wang and Weathers 2009. [5] Bortolotti and Wiebe 1993. [6] Wiebe et al. 1998b. [7] Afton 1980. [8] Poussart et al. 2000. [9] Ashkenazie and Safriel 1979.

predictions, the anseriforms displayed only slow-rise patterns (Table 4) and the sole precocial non-anseriform, the Semipalmated Sandpiper (*Calidris pusilla*), exhibited only rapid-rise patterns.

The predictions are less clear-cut when laying-stage nest attendance cannot be distinguished from effective incubation. One might expect that synchronously hatching altricial species would be more likely to display rapid-rise patterns that start with the last egg, but any type of pattern is theoretically possible if laying-stage nest attendance does not accelerate embryo development. None of the altricial species could conclusively be called synchronous, because the upper end of hatching spans reported from these studies exceeded 24 h. The Mountain White-crowned Sparrow exhibited only the slow-rise pattern; the other five species from our previous study displayed slow-rise and flat-rise patterns more frequently than rapid-rise.

Asynchronously hatching species are more likely to have laying-stage nest attendance that provides effective incubation. Although any type of rising pattern can be expected, the amount of laying-stage incubation should then be reflected in the degree of hatching asynchrony. Asynchronously hatching species did not show consistent patterns of incubation onset. The altricial Green-rumped Parrotlet predominantly exhibited rising patterns, whereas the semi-altricial American Kestrel (*Falco sparverius*) was mostly represented by rising patterns and the Eurasian Kestrel (*F. tinnunculus*) by irregular rising patterns. Although laying-stage nest attendance was correlated with the degree of hatching asynchrony in the Eurasian Kestrel (Wiebe et al. 1998b) and with hatching order in the Green-rumped Parrotlet (Grenier and Beissinger 1999), it did not account for hatching order in the American Kestrel (Bortolotti and Wiebe 1993).

Some patterns seem to be products of unfavorable conditions specific to the individual or laying period, such as poor body condition or harsh environmental conditions (Wiebe et al. 1998b), and may result in decreased hatching success (Wang and Beissinger 2009). We previously classified these patterns into the irregular-rising and not-rising groups (Fig. 1). One might expect that these groups would not vary predictably with mode of development, hatching pattern, or taxonomic order. The irregular-rising group of patterns was generally less common and taxonomically unbiased in representation. Not-rising was the least common group; its patterns appeared in only one individual from each of three species. Hence, these patterns seem to be the result of constraints on adult behavior rather than strategies or tactics.

To summarize, in species in which nest attendance during the laying stage results in effective incubation, patterns of the onset of incubation reflect hatching patterns and the degree of hatching asynchrony. But these relationships break down when nest attendance in the laying stage does not correlate with effective incubation. If individual variation is as great as these data indicate, individual, environmental, and taxonomic factors may all influence developmental trajectories of incubation at different temporal scales.

SUGGESTIONS FOR REPORTING INCUBATION DATA

Standardized criteria for determining the onset of full incubation would facilitate interspecific comparisons of incubation from studies using disparate methods of quantifying incubation.

We recommend using a 90% lower confidence interval of daily or nightly attentiveness, calculated starting with the day or night after clutch completion, as a threshold for the onset of full incubation (Wang and Beissinger 2009). If egg temperatures are available, then the lower 90% confidence interval of the mean daily (or nightly) egg temperature after clutch completion could be used. This criterion is estimated in relation to the incubation behavior (or egg temperature) at each nest after the laying period, and quantifies what many studies have done implicitly by plotting daily attentiveness or mean egg temperatures through the laying and incubation periods. With the variety of continuous-data-recording technologies available today, there are few limitations on obtaining daily attentiveness during and well past the laying period.

As far as labeling when the onset of incubation occurs, researchers have used either the first egg as the reference (first, second, third, etc.) or the last egg as the reference (ultimate, penultimate, prepenultimate, etc.). The choice often depends on the species' hatching pattern, because asynchronous species commonly begin full incubation closer to the first half of the laying period and synchronous species start full incubation in the second half of the laying period. The onset of partial incubation is often reported using the first egg as the reference, because onset is more likely to occur early in the laying period. Unfortunately, eggs that have the same label with reference to the last egg can have different numbers of eggs preceding them, depending on the clutch size. We propose a labeling protocol that incorporates both types of names (Table 5). The protocol can easily be applied to clutches of 1 to 7 or more and applies unambiguous labels to both ends of the clutch. We hope that this modified protocol will allow for easier cross-study comparisons in the future.

The causes of variation in incubation onset patterns largely remain to be determined (Wang and Beissinger 2009). These include forces that act within individuals or nests on a small temporal scale (daily changes in environmental conditions or energetic constraints on adults), among individuals or nests (age, body condition, experience), and through larger-scale environmental variation (yearly or seasonal change). Mixed models can incorporate autocorrelation in repeated observations within individuals as well as correlations across individuals that are explained by variables such as age (Diggle et al. 2002). For linear trajectories, differences in slope and elevation can be attributed to fixed effects, such as year and age, or random effects based on individual variables such as condition (Littell et al. 2006). Variables that change value daily, such as ambient temperature, humidity, and precipitation, can be incorporated as time-varying covariates. These approaches allow multiple temporal scales to be investigated simultaneously (e.g., daily, seasonal, or yearly) with "permanent" environmental effects over an individual's lifetime.

FERTILE AREAS FOR FUTURE RESEARCH

The extent and causes of partial incubation are poorly understood. Although partial incubation is more common than previously recognized, there is no consensus on what it is or what it does. Investigating proximate influences on partial incubation also addresses questions about patterns of full incubation onset. Genetic, physiological, and environmental factors will provide the underpinnings of variation in incubation onset, and may also illuminate constraints on the evolution of incubation strategies. Individual-level behavioral data related to variation in the onset of incubation could address a host of questions at both the intraspecific and interspecific levels. Does intraspecific variation in the onset of incubation correlate with the size of a species' geographic range or with temporal variability in weather during the breeding season? Does partial incubation vary substantially within all species, or are some taxa less flexible in this trait? Additionally, does partial incubation vary with the proportion of nests lost to predators or starvation, between cavity- and open-cup-nesting species, or between species with single-sex versus biparental incubation?

At the proximate level, partial incubation can be viewed as the behavioral outcome of physiological changes during the laying period (Mead and Morton 1985, Sockman et al. 2006). A gradual increase in prolactin often accompanies a gradual increase in incubation behavior; individual trajectories of incubation constancy during egg laying should then mirror those of prolactin levels (Sockman et al. 2000). This view predicts that incubation constancy should covary with prolactin levels, which in turn may be related to individual factors, such as body condition, age, and

TABLE 5. Proposed labeling protocol for the onset of incubation. For species with laying intervals of 1 day, labels would indicate onset for the day on which the egg is laid. For species with laying intervals greater than 1 day, labels would indicate the number of eggs in the nest at onset. For clutches of more than 7 eggs, the label "middle" would be repeated as needed for eggs laid in intermediate positions. Despite an attempt to assign fixed labels to every egg position for all clutch sizes, some ambiguity remains: labels in parentheses within a row indicate equivalent terms that may be chosen depending on the other clutch sizes in a particular study. For instance, if all clutches greater than 1 egg began full incubation with the last egg laid, the sole 1-egg clutch may be said to have an onset of incubation with the last egg laid instead of the first egg laid, for ease of comparison.

Clutch size	Egg label						
1	(First)	—	—	—	—	—	(Last)
2	First	—	—	—	—	—	Last
3	First	(Second)	—	—	—	(Penultimate)	Last
4	First	Second	—	—	—	Penultimate	Last
5	First	Second	(Third)	—	(Prepenultimate)	Penultimate	Last
6	First	Second	Third	—	Prepenultimate	Penultimate	Last
≥7	First	Second	Third	Middle	Prepenultimate	Penultimate	Last

prior breeding experience. Whether rapid behavioral changes in nest attendance or incubation are accompanied by physiological shifts in hormone levels has not been thoroughly studied (Jónsson et al. 2006). In species in which both sexes incubate, plasma prolactin levels remain high during extended absences from the nest (Vleck et al. 2000), which suggests interspecific variability in the relationship between prolactin and parental behavior. Species with biparental incubation may have onset patterns that are less tightly coupled to hormone levels.

Short-term behavioral lability in the development of incubation offers a window into the tradeoffs among adult survival, maintenance, and reproduction. Not only do daily behavioral changes reflect shifts in the balance of energy or time allotted to maintenance or reproduction, but these shifts directly affect offspring survival and quality (Wang and Beissinger 2009). As such, patterns in the onset of incubation interact with other labile reproductive traits, such as clutch size and lay date, to integrate past and current environmental conditions into a combined reproductive effort.

Solving the methodological issues for studying the onset of incubation may ultimately provide a window into the evolution of hatching patterns. Depending on the environmental conditions, either nest attendance or true incubation may be necessary to preserve egg viability. Discovering the types and patterns of early incubation may help explain latitudinal gradients in hatching asynchrony (Clark and Wilson 1981), hatchability (Koenig 1982), and clutch size (Cooper et al. 2006, Jetz et al. 2008).

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Supplementary Online Material for

PARTIAL INCUBATION IN BIRDS: ITS OCCURRENCE, FUNCTION, AND QUANTIFICATION

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APPENDIX. Species studied for the onset of full incubation ($n = 123$ samples), with information on the onset of partial incubation when known.

Species[a]	Egg with which partial incubation starts[b,c]	Egg with which full incubation starts[b]	Mode of development[d]	Hatching pattern[e]	Continuous data?[f]	Egg with which data started[g]	n[h]	Source
Snow Goose (*Chen caerulescens*)	Second	Last	Precocial	Synchronous	Y	1–2	7	Poussart et al. (2000)
Barnacle Goose (*Branta leucopsis*)	Not stated	First to last	Precocial	Synchronous	Y	1–2	6	Hubner et al. (2002)
(Whistling) Tundra Swan (*Cygnus columbianus columbianus*)	First	Second	Precocial	Synchronous	Y	1	1	Hawkins (1986)
Mallard (*Anas platyrhynchos*)	Sixth (middle)	Last	Precocial	Synchronous	Y	1+X	3	Caldwell and Cornwell (1975)
Northern Shoveler (*Anas clypeata*)	Not stated	Last, after last	Precocial	Synchronous	Y	1+X	4	Afton (1980)
Common Eider (*Somateria mollissima mollissima*)	No data	Prepenultimate, penultimate	Precocial	Synchronous	Y	1	17	Hanssen et al. (2002)
Common Goldeneye (*Bucephala clangula*)	No data	Fifth (middle)	Precocial	Synchronous	Y	?	16	Mallory and Weatherhead (1993)
Ring-necked Pheasant (*Phasianus colchicus*)	Fifth (middle)	Last (most common)	Precocial	Synchronous	Y	1+X	14	Persson and Göransson (1999)
Willow Ptarmigan (*Lagopus lagopus*)	Pre-antepenultimate (middle)	Penultimate	Precocial	Synchronous	Y	1+X	1	Pulliainen (1978)
Adélie Penguin (*Pygoscelis adeliae*)	First	Last	Semi-precocial	Asynchronous	Y	1	12	Derksen (1977)
Gentoo Penguin (*Pygoscelis papua*)	First	Second (last)	Semi-precocial	Asynchronous	Y	1–2	?	Burger and Williams (1979)
Jackass Penguin (*Spheniscus demersus*)	First	Second (last)	Semi-precocial	Asynchronous	Y	1–2	?	Burger and Williams (1979)
Fiordland Penguin (*Eudyptes pachyrhynchus*)	First	Last	Semi-precocial	Syn-asyn	N	1	16	St. Clair (1992)
Macaroni Penguin (*Eudyptes chrysolophus*)	First	After last	Semi-precocial	NA	Y	1–2	?	Burger and Williams (1979)

(continued)

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Appendix. Continued.

Species[a]	Egg with which partial incubation starts[b,c]	Egg with which full incubation starts[b]	Mode of development[d]	Hatching pattern[e]	Continuous data?[f]	Egg with which data started[g]	*n*[h]	Source
Rockhopper Penguin (*Eudyptes chrysocome*)	First	After last	Semi-precocial	Asynchronous	Y	1–2	10	Burger and Williams (1979)
Fork-tailed Storm-Petrel (*Oceanodroma furcata*)	NA	First	Precocial	NA	Y	1	19	Simons (1981)
Least Bittern (*Ixobrychus exilis*)	NA	First, second	Semi-altricial	Asynchronous	N	1	4	Weller (1961)
Black Kite (*Milvus migrans*)	No data	Penultimate	Semi-altricial	Asynchronous	N	1	37	Viñuela (1997)
Eurasian Kestrel (*Falco tinnunculus*)	Not stated	Penultimate, last	Semi-altricial	Asynchronous	Y	1–2	17	Wiebe et al. (1998)
American Kestrel (*Falco sparverius*)	First	Penultimate, last	Semi-altricial	Asynchronous	Y	1	4	Bortolotti and Wiebe (1993)
American Kestrel	Not stated	Last	Semi-altricial	Asynchronous	Y	1–2	2	Sockman and Schwabl (1998)
American Kestrel	First	First	Semi-altricial	Asynchronous	Y	1–2	5	Sockman et al. (2000)
Senegal Lapwing (*Vanellus lugubris*)	No data	First	Precocial	Synchronous	Y	1	3	Ward (1990)
Black-winged Lapwing (*Vanellus melanopterus*)	No data	After last	Precocial	Synchronous	Y	?	3	Ward (1990)
Crowned Lapwing (*Vanellus coronatus*)	No data	First, last	Precocial	Synchronous	Y	1	7	Ward (1990)
Spotted Sandpiper (*Actitis macularius*)	First	Third	Precocial	Synchronous	N	1	34	Maxson and Oring (1980)
Long-billed Curlew (*Numenius americanus*)	No data	After last	Precocial	Synchronous	N	1+X	2	Allen (1980)
Long-billed Curlew	Not stated	Penultimate	Precocial	Synchronous	Y	1+X	18	Hartman and Oring (2006)
Semipalmated Sandpiper (*Calidris pusilla*)	First	Last	Precocial	Synchronous	Y	1	4	Ashkenazie and Safriel (1979)
Semipalmated Sandpiper	Second	Last	Precocial	Synchronous	N	?	2	Norton (1972)
Baird's Sandpiper (*Calidris bairdii*)	Second	Last	Precocial	Asynchronous	Y	?	7	Norton (1972)
Pectoral Sandpiper (*Calidris melanotos*)	No data	Last	Precocial	Synchronous	Y	?	4	Norton (1972)
Dunlin (*Calidris alpina*)	Penultimate	Last	Precocial	Syn-asyn	Y	?	4	Norton (1972)
Egyptian Plover (*Pluvianus aegyptius*)	No data	First	Precocial	Synchronous	Y	1–2	2	Howell (1979)
Black-legged Kittiwake (*Rissa tridactyla*)	Not stated	Last	Semi-precocial	Syn-asyn	Y	1	10	Barrett (1980)
Black-legged Kittiwake	First	First	Semi-precocial	Syn-asyn	Y	1	8	Coulson and Wooller (1984)
Black-headed Gull (*Chroicocephalus ridibundus*)	First	Last	Semi-precocial	Synchronous	N	1	?	Beer (1962)
Mew Gull (*Larus canus*)	First	Last, after last	Semi-precocial	Synchronous	Y	1	3	Barth (1955)
Xantus's Murrelet (*Synthliboramphus hypoleucus*)	NA	After last	Precocial	Synchronous	N	1	51	Murray et al. (1983)
Ruddy Ground-Dove (*Columbina talpacoti*)	NA	First	Altricial	Syn-asyn	N	1	2	Skutch (1956)
Croaking Ground-Dove (*Columbina cruziana*)	No data	First	Altricial	Syn-asyn	N	1	?	Marchant (1959)
Blue Ground-Dove (*Claravis pretiosa*)	NA	First	Altricial	Synchronous	N	1	1	Skutch (1959)
Budgerigar (*Melopsittacus undulatus*)	No data	First	Altricial	Asynchronous	N	1	?	Wyndham (1981)

(*continued*)

APPENDIX. Continued.

Species[a]	Egg with which partial incubation starts[b,c]	Egg with which full incubation starts[b]	Mode of development[d]	Hatching pattern[e]	Continuous data?[f]	Egg with which data started[g]	*n*[h]	Source
Green-rumped Parrotlet (*Forpus passerinus*)	First	Third to prepenultimate	Altricial	Asynchronous	Y	1–2	12	Grenier and Beissinger (1999)
Pacific Parrotlet (*Forpus coelestis*)	First?	Second	Altricial	Asynchronous	N	?	?	Marchant (1960)
Madagascar Coucal (*Centropus toulou*)	NA	First	Altricial	Asynchronous	N	1	1	Frith (1975)
Common Swift (*Apus apus*)	No data	Second	Altricial	Syn-asyn	N	1	?	Lack and Lack (1951)
Rufous-breasted Hermit (*Glaucis hirsutus*)	First	Second	Altricial	Asynchronous	N	1	?	Snow (1973), Snow and Snow (1973)
Short-tailed Woodstar (*Myrmia micrura*)	First?	Second	Altricial	Synchronous	N	?	?	Marchant (1960)
Speckled Mousebird (*Colius striatus*)	NA	First	Altricial	Asynchronous	N	1	?	Rowan (1967)
White-backed Mousebird (*Colius colius*)	NA	First	Altricial	Asynchronous	N	1	?	Rowan (1967)
Red-faced Mousebird (*Urocolius indicus*)	NA	First	Altricial	Asynchronous	N	1	?	Rowan (1967)
European Bee-eater (*Merops apiaster*)	First	Last	Altricial	Asynchronous	N	1	17	Lessells and Avery (1989)
Eurasian Hoopoe (*Upupa epops*)	No data	First	Altricial	Synchronous	N	1	?	Skead (1950)
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	Second	Last	Altricial	Asynchronous	N	1	2	Jackson (1976)
Red-bellied Woodpecker (*Melanerpes carolinus*)	Second	Last	Altricial	Asynchronous	N	1	1	Jackson (1976)
Bicolored Antbird (*Gymnopithys leucaspis*)	Second (last)	After last	Altricial	Asynchronous	N	1+X	?	Willis (1973)
Sclater's Tyrannulet (*Phyllomyias sclateri*)	No data	Last	Altricial	Syn-asyn	N	1	2	Marchant (1960)
Dusky Flycatcher (*Empidonax oberholseri*)	First	Prepenultimate, penultimate	Altricial	Asynchronous	Y	1	9	Morton and Pereyra (1985)
Pacific-slope Flycatcher (*Empidonax difficilis*)	Before last	Last	Altricial	Asynchronous	N	1	9	Davis et al. (1963)
Ash-throated Flycatcher (*Myiarchus cinerascens*)	Second, third	After last	Altricial	Syn-asyn	Y	1	8	Wang and Beissinger (2009)
White-bearded Flycatcher (*Phelpsia inornata*)	NA	First	Altricial	Asynchronous	N	1	1	Thomas (1979)
Superb Lyrebird (*Menura novaehollandiae*)	First (last)	After last	Altricial	NA	Y	1	6	Lill (1979)
Noisy Miner (*Manorina melanocephala*)	No data	Second	Altricial	Asynchronous	N	?	2	Dow (1978)
Tree Swallow (*Tachycineta bicolor*)	First, second	Penultimate to after last	Altricial	Syn-asyn	Y	1	17	Wang and Beissinger (2009)
Violet-green Swallow (*Tachycineta thalassina*)	First, second	Penultimate to after last	Altricial	Syn-asyn	Y	1	10	Wang and Beissinger (2009)
Barn Swallow (*Hirundo rustica*)	No data	Penultimate	Altricial	Asynchronous	N	1	1	Smith (1933)
Barn Swallow	Second, third	Penultimate	Altricial	Synchronous	N	1	?	Samuel (1971)
Barn Swallow	No data	Prepenultimate, penultimate	Altricial	Syn-asyn	N	?	16	Banbura and Zielinski (1995)
Welcome Swallow (*Hirundo neoxena*)	No data	Last	Altricial	No data	N	1	10	Crouchley and Crouchley (1979)

(*continued*)

Appendix. Continued.

Species[a]	Egg with which partial incubation starts[b,c]	Egg with which full incubation starts[b]	Mode of development[d]	Hatching pattern[e]	Continuous data?[f]	Egg with which data started[g]	*n*[h]	Source
Cliff Swallow (*Petrochelidon pyrrhonota*)	Second, third	Penultimate	Altricial	Synchronous	N	1	?	Samuel (1971)
Marsh Tit (*Poecile palustris*)	No data	Penultimate to after last	Altricial	Syn-asyn	N	1	23	Nilsson (1993)
Willow Tit (*Poecile montanus*)	Penultimate, last	After last	Altricial	Syn-asyn	Y	1+X	4	Haftorn (1979)
Carolina Chickadee (*Poecile carolinensis*)	No data	Penultimate, last	Altricial	Synchronous	N	1+X	?	Brewer (1961)
Black-capped Chickadee (*Poecile atricapillus*)	No data	Penultimate	Altricial	Synchronous	N	?	1	Odum (1941)
Black-capped Chickadee	No data	Penultimate	Altricial	Synchronous	N	1+X	?	Brewer (1961)
Boreal Chickadee (*Poecile hudsonicus*)	No data	Penultimate, last	Altricial	Syn-asyn	N	?	4	McLaren (1975)
Great Tit (*Parus major*)	Prepenultimate	Prepenultimate to after last	Altricial	Asynchronous	N	1	57	Gibb (1950)
Great Tit	Third to sixth	Last, after last	Altricial	Asynchronous	Y	1	37	Haftorn (1981)
Eurasian Blue Tit (*Cyanistes caeruleus*)	No data	Middle to after last	Altricial	Asynchronous	N	1	47	Gibb (1950)
Eurasian Blue Tit	Prepenultimate	Penultimate	Altricial	No data	Y	?	2	Haftorn and Reinertsen (1985)
Eurasian Blue Tit	No data	Penultimate, last (most common)	Altricial	Syn-asyn	N	1	54	Nilsson (1993)
Oak Titmouse (*Baeolophus inornatus*)	Second to sixth	Last, after last	Altricial	Syn-asyn	Y	1	12	Wang and Beissinger (2009)
House Wren (*Troglodytes aedon*)	First	Last	Altricial	Syn-asyn	Y	?	5	Kendeigh (1963)
Goldcrest (*Regulus regulus*)	Second, middle	Prepenultimate	Altricial	Asynchronous	Y	1+X	2	Haftorn (1978)
European Pied Flycatcher (*Ficedula hypoleuca*)	No data	Penultimate, last (most common)	Altricial	Syn-asyn	N	1	155	Potti (1998)
Eastern Bluebird (*Sialia sialis*)	No data	Last	Altricial	Syn-asyn	N	?	?	Hamilton (1943)
Western Bluebird (*Sialia mexicana*)	Second to fourth	Last, after last	Altricial	Syn-asyn	Y	1	26	Wang and Beissinger (2009)
Western Bluebird	Not stated	After last	Altricial	Syn-asyn	Y	1+X	6	Wang and Weathers (2009)
Wood Thrush (*Hylocichla mustelina*)	First to penultimate	Penultimate	Altricial	Asynchronous	N	1	14	Brackbill (1958)
Eurasian Blackbird (*Turdus merula*)	First	Last	Altricial	Asynchronous	Y	1	2	Gurr (1954)
Eurasian Blackbird	No data	First to penultimate	Altricial	Syn-asyn	N	1+X	?	Snow (1958)
Eurasian Blackbird	No data	Penultimate, last	Altricial	Asynchronous	N	1	178	Magrath (1992)
Song Thrush (*Turdus philomelos*)	Second	Last	Altricial	Synchronous	Y	1	1	Marples and Gurr (1943)
American Robin (*Turdus migratorius*)	No data	First to last	Altricial	Asynchronous	N	1	?	Howell (1942)
American Robin	No data	First to after last	Altricial	Asynchronous	N	1	128	Rowe and Weatherhead (2009)

(*continued*)

Appendix. Continued.

Species[a]	Egg with which partial incubation starts[b,c]	Egg with which full incubation starts[b]	Mode of development[d]	Hatching pattern[e]	Continuous data?[f]	Egg with which data started[g]	*n*[h]	Source
Cedar Waxwing (*Bombycilla cedrorum*)	First	After last	Altricial	Asynchronous	N	1	2	Putnam (1949)
Yellow Warbler (*Setophaga petechia*)	Prepenultimate	Last, after last	Altricial	Asynchronous	N	1+X	31	Hébert and Sealy (1992)
Ovenbird (*Seiurus aurocapilla*)	No data	Penultimate	Altricial	No data	N	1	?	Hann (1937)
Painted Redstart (*Myioborus pictus*)	No data	Penultimate to after last	Altricial	Syn-asyn	N	?	4	Marshall and Balda (1974)
American Tree Sparrow (*Spizella arborea*)	Not stated	Penultimate	Altricial	Syn-asyn	Y	?	5	Stenger Weeden (1966)
Chipping Sparrow (*Spizella passerina*)	No data	Penultimate, last	Altricial	Syn-asyn	N	1+X	4	Walkinshaw (1944)
Field Sparrow (*Spizella pusilla*)	No data	Penultimate	Altricial	Syn-asyn	N	1+X	?	Walkinshaw (1939)
(Mountain) White-crowned Sparrow (*Zonotrichia leucophrys oriantha*)	First	Last, after last	Altricial	Syn-asyn	N	1	?	Morton et al. (1972)
(Mountain) White-crowned Sparrow	First	Last	Altricial	Syn-asyn	Y	1	9	Zerba and Morton (1983)
McCown's Longspur (*Rhynchophanes mccownii*)	No data	Penultimate	Altricial	Syn-asyn	N	1+X	3	Mickey (1943)
Smith's Longspur (*Calcarius pictus*)	No data	Last	Altricial	Syn-asyn	N	?	3	Jehl (1968)
Red-winged Blackbird (*Agelaius phoeniceus*)	First	Penultimate	Altricial	Asynchronous	Y	1	5	Holcomb (1974)
Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*)	No data	First, second	Altricial	Asynchronous	N	1	74	Fautin (1941)
House Finch (*Carpodacus mexicanus*)	Not stated	Penultimate, last	Altricial	Syn-asyn	N	?	?	Evenden (1957)
House Finch	Not stated	First to last	Altricial	Syn-asyn	Y	1	33	Badyaev et al. (2003), Alabama site
House Finch	Not stated	First to last	Altricial	Syn-asyn	Y	1	31	Badyaev et al. (2003), Montana site
Pine Siskin (*Spinus pinus*)	No data	First	Altricial	Syn-asyn	N	1	1	Weaver and West (1943)
House Sparrow (*Passer domesticus*)	No data	Prepenultimate, penultimate	Altricial	Syn-asyn	N	?	?	Weaver (1943)
House Sparrow	No data	First	Altricial	Syn-asyn	N	1+X	?	Seel (1968)
House Sparrow	First	Prepenultimate to last	Altricial	Asynchronous	Y	1	5	Anderson (1997)
Eurasian Tree Sparrow (*Passer montanus*)	No data	First	Altricial	Syn-asyn	N	1	?	Seel (1968)
Black-cheeked Waxbill (*Estrilda erythronotos*)	No data	First	Altricial	No data	N	1	?	Skead (1975)
Blue-breasted Cordonbleu (*Uraeginthus angolensis*)	No data	First	Altricial	No data	N	1	?	Skead (1975)
Violet-eared Waxbill (*Granatina granatina*)	No data	First	Altricial	No data	N	1	?	Skead (1975)
Green-winged Pytilia (*Pytilia melba*)	No data	First	Altricial	No data	N	1	?	Skead (1975)

(*continued*)

Appendix. Continued.

Species[a]	Egg with which partial incubation starts[b,c]	Egg with which full incubation starts[b]	Mode of development[d]	Hatching pattern[e]	Continuous data?[f]	Egg with which data started[g]	n[h]	Source
Zebra Finch (*Taeniopygia guttata*)	First	Third	Altricial	Asynchronous	Y	1	14	El-Wailly (1966)
Black-throated Finch (*Poephila cincta*)	Before fourth	Prepenultimate to last	altricial	Asynchronous	N	?	?	Zann (1976)

[a] Common and scientific names follow the Clements Checklist 6.5 (Clements et al. 2010).

[b] Based on terminology used in the source. Terms based on Table 5 are shown in parentheses if different from those of the source.

[c] No data = data did not allow determination. Not stated = data may have allowed determination, but onset of partial incubation was not stated. NA = not applicable (full incubation began with the first egg laid).

[d] Follows Nice (1962), as cited by Baicich and Harrison (1997).

[e] Asynchronous = hatching span >24 h, synchronous = hatching span ≤24 h, syn-asyn = hatching spans varying from <24 h to >24 h. NA = not applicable (for species laying a one-egg clutch).

[f] Did the method of data collection allow a continuous record of events to be reconstructed? Y = yes, N = no.

[g] 1 = first egg, 1–2 = first and second eggs, 1+X = later than first egg or varied, ? = not stated.

[h] Sample size used to determine the onset of incubation. ? = unclear or not stated.

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