Adaptive specialization, conditional plasticity and phylogenetic history in the reproductive cue response systems of birds

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Appropriately timed integration of breeding into avian annual cycles is critical to both reproductive success and survival. The mechanisms by which birds regulate timing of breeding depend on environmental cue response systems that regulate both when birds do and do not breed. Despite there being multiple possible explanations for birds' abilities to time breeding appropriately in different environments, and for the distribution of different cue response system characteristics among taxa, many studies infer that adaptive specialization of cue response systems has occurred without explicitly considering the alternatives. In this paper, we make explicit three hypotheses concerning the timing of reproduction and distribution of cue response characteristics among taxa: adaptive specialization; conditional plasticity; and phylogenetic history. We emphasize in particular that although conditional plasticity built into avian cue response systems (e.g. differing rates of gonadal development and differing latencies until onset of photorefractoriness) may lead to maladaptive annual cycles in some novel circumstances, this plasticity also can lead to what appear to be adaptively specialized cue response systems if not viewed in a comparative context. We use a comparative approach to account for the distribution of one important feature of avian reproductive cue response systems, photorefractoriness. Analysis of the distribution within songbirds of one criterion for absolute photorefractoriness, the spontaneous regression of the gonads without any decline in photoperiod, reveals that a failure to display this trait probably represents an adaptive specialization to facilitate a flexible reproductive schedule. More finely resolved analysis of both criteria for absolute photorefractoriness (the second being total lack of a reproductive response even to constant light after gonadal regression has occurred) within the cardueline finches not only provides further confirmation of this interpretation, but also indicates that these two criteria for photorefractoriness can be, and have been, uncoupled in some taxa. We suggest that careful comparative studies at different phylogenetic scales will be extremely valuable for distinguishing between adaptive specialization and non-adaptive explanations, such as phylogenetic history as explanations of cue response traits in particular taxa. We also suggest that particular focus on taxa in which individuals may breed on very different photoperiods (latitudes or times of year) in different years should be particularly valuable in identifying the range of environmental conditions across which conditionally plastic cue responses can be adaptive.

Keywords: seasonal breeding; photoperiodism; photorefractoriness; environmental cues; songbird

1. INTRODUCTION: TIMING OF BREEDING AND 'FIT' TO DIFFERENT ENVIRONMENTS

A basic goal in biology is to understand how organisms come to be 'well suited' to their environments (Fretwell 1972). From a fitness standpoint, the choice of when to breed is a key indicator of being well suited to an environment, since timing of breeding affects both the likelihood of producing high-quality offspring and the probability of adult survival (Drent & Daan 1980; Farner *et al.* 1983; Svensson 1997; McNamara *et al.* 2004; Komdeur & Daan 2005; Verhulst & Nilsson 2008). In environments where conditions vary in space

and time (i.e. most environments), the reproductive schedule should track changes in ultimate environmental factors (e.g. food supply, weather) that affect reproductive success (Baker 1938; Perrins 1970). Consequently, selection should favour individuals that possess mechanisms permitting them to detect and respond to proximate cues that predict impending relevant changes in the environment (Baker 1938). Processing of such cues is achieved by the neuroendocrine system, which transduces information from both external cues (e.g. changing day length, rainfall, food supply) and internal processes (e.g. the readout from circannual clocks and modulation, if any, of responsiveness to environmental cues) into neuroendocrine signals that regulate changes in reproductive physiology, morphology and behaviour (e.g. Follett 1984; Ball 1993).

Appropriate timing of reproduction in a particular environment clearly could be achieved if the

neuroendocrine cue processing system is adaptively specialized to be particularly effective at tracking the environmental changes that occur in that environment. However, reproductive schedules well suited to specific environments do not necessarily require specific adaptations of the neuroendocrine cue processing system to the details of those environments. Appropriate reproductive timing also may occur if the neuroendocrine cue processing system's conditional plasticity (how it responds to different patterns of cues) facilitates effective tracking of changes in a variety of environments, including the one the animal happens to occupy (the jack of all trades; cf. Huey & Hertz 1984). Further, neuroendocrine cue processing systems also may exhibit features retained through phylogenetic history but not specifically related to timing of reproduction in the current environment. Such features may exist as neutral traits and may be potential preadaptations or may have been adaptive for ancestral species. Thus, determining whether species possess specific adaptations to facilitate appropriate timing of reproduction requires consideration of three different hypotheses:

> (i) *Adaptive specialization hypothesis*. Species possess cue response systems with features that represent specialized adaptations to the details of the environment occupied.
> (ii) *Conditional plasticity hypothesis*. Species possess cue response systems that can generate a range of appropriate responses depending on conditions experienced, and therefore can time reproduction appropriately in a range of environments.
> (iii) *Phylogenetic history hypothesis*. Features of the cue response system are retained by evolutionary descent and may not be specifically adaptive in the current environment.

Decades of research on the mechanisms by which birds process environmental cues to time reproduction, beginning with the pioneering studies of Rowan (1925, 1926), provide a basis for evaluating the extent to which adaptive natural reproductive schedules in different taxa result from adaptive specializations of cue response patterns and mechanisms or, alternatively, emerge from conditionally plastic outputs of interspecifically similar cue response characteristics. This issue has been of interest for many years and is the subject of some excellent and stimulating older reviews (e.g. Lofts & Murton 1968; Farner *et al.* 1983; Nicholls *et al.* 1988) that are still highly pertinent. However, for several reasons, it is appropriate now to revisit the question of adaptive specialization of reproductive cue response systems. First, substantial new empirical data are available, some of which specifically speak to the phenomenon of local adaptation of environmental cue response systems (e.g. Lambrechts *et al.* 1996, 1997) and to the evolutionary mechanisms that would facilitate such adaptation (e.g. Coppack *et al.* 2003; Coppack & Pulido 2004). Second, the advent of quantitative comparative methods (e.g. Felsenstein 1985; Harvey & Pagel 1991) permits a more rigorous assessment of the likelihood that interspecies differences either in cue response patterns or in underlying

mechanisms represent specific adaptations to different environments as opposed to being accounted for at least in part by non-adaptive explanations, such as phylogenetic history (MacDougall-Shackleton *et al.* 2005). Third, the current interest in how global climate change may affect different populations warrants specific consideration of how different species' cue response systems may facilitate or hinder adjustment of breeding schedules to changing environmental conditions (e.g. Coppack & Both 2002; Coppack & Pulido 2004).

The intent of this paper is not to perform either an exhaustive review of existing empirical data on avian reproductive cue response systems or an exhaustive comparative analysis of it. Instead we review briefly the history of evaluations of adaptive specialization of avian reproductive cue response systems, with particular emphasis on the regulation of reproductive development prior to breeding and of gonadal collapse at the end of breeding, and examine the three alternative hypotheses—adaptive specialization, conditional plasticity and phylogenetic history—enunciated above. We suggest that these should be considered explicitly when contemplating the adaptive significance of patterns of reproductive schedules and mechanisms among species. These hypotheses have not, to our knowledge, been applied to avian reproductive timing patterns and mechanisms; reviews of the topic to date generally assume specialized adaptations without explicitly considering any alternatives (e.g. Lofts & Murton 1968; Farner *et al.* 1983). In fact, it is difficult to find papers on avian cue response patterns and mechanisms that do *not* report support for what amounts to adaptive specialization despite lacking any discussion of possible alternative explanations. It is important to keep in mind that environmental cue response systems are also involved in the regulation of actual onset of nesting once reproductive development is complete, as well as in the coordination of the complex sequence of behavioural and physiological events that occur within nesting cycles (Wingfield 1980, 1983); we do not deal with those interesting processes here.

To illustrate the value of the approach we suggest, we will perform a limited comparison of a prominent and important feature of many birds' reproductive cue response systems, the development of a state of photorefractoriness, which has presumably evolved (perhaps multiple times; Farner *et al.* 1983) to terminate and then prevent breeding so as to facilitate adult survival, and minimize wasted reproductive effort on broods with little chance of survival, in seasonal environments at mid to high latitudes. Two different criteria have been used to detect photorefractoriness, spontaneous gonadal regression on long days and complete lack of reproductive responsiveness to very long days once regression has occurred (Farner *et al.* 1983; see below for details). We will compare the first criterion among songbirds generally and will compare both criteria within one tribe of songbirds, the cardueline finches, in more detail. We will finish the paper with a discussion of the implications of our conceptual framework and comparative findings for evolution, colonization of new areas and responses to climate change.

2. DIVERSITY OF AVIAN CUE RESPONSE PATTERNS AND MECHANISMS

Intertaxon diversity of reproductive cue response patterns and mechanisms has interested avian endocrinologists for many years. Following Rowan's discoveries of photoresponsiveness (1925, 1926) in juncos (*Junco hyemalis*), data accumulated rapidly on a number of other temperate zone taxa, and broad similarities (reviewed especially by Nicholls *et al.* 1988) and differences (e.g. Lofts & Murton 1968; Farner *et al.* 1983) among taxa quickly became evident. There was, for a time, particular interest in whether tropical and temperate zone taxa might have evolved to differ fundamentally from one another (e.g. Marshall & Disney 1957; Farner & Serventy 1960). Since tropical and desert-dwelling taxa occupy environments where photoperiod either changes very little, presumably rendering seasonal changes difficult to measure, or where it is apparently uncorrelated with changes in ultimate factors dictating reproductive success, rendering it useless as a predictive cue even if changes could be measured, day length was thought to be of little use to such species (e.g. Lofts & Murton 1968). This idea directed attention to non-photic cues, such as weather, temperature and food supply, and a number of studies demonstrated effects of non-photic cues on avian reproduction in tropical and xerophilous birds, as well as in 'typical' seasonal taxa of higher latitudes (reviewed by Marshall 1970; see also Ligon 1974; Jones & Ward 1976). Interest in how non-photic cues are integrated with long-term predictive cues like photoperiod has persisted (e.g. Wingfield 1980, 1983; Wingfield *et al.* 1992, 1993, 1996, 1997, 2003; Hau *et al.* 2000; Hau 2001; Hahn *et al.* 2005). Nevertheless, surprisingly strong photoperiodic responses were found early on in some tropical and desert-dwelling taxa (e.g. Vaugien 1952, 1953; Marshall & Disney 1956; see also Gwinner & Dittami 1985), and subsequent research clearly shows that tropical birds respond to sufficiently small changes in photoperiod to be able to use this cue to help time breeding (Hau *et al.* 1998; Misra *et al.* 2004; Styrsky *et al.* 2004; see also Rani *et al.* 2005*b*). Although this finding may seem to support the idea of adaptive specialization of cue response systems in different environments (which it may), it also illustrates well the importance of considering alternative explanations: sensitivity to small differences in photoperiod in tropical taxa does not necessarily represent a specific adaptation to facilitate the use of photoperiod at low latitudes. Many (perhaps all) higher-latitude photoperiodic species display striking sensitivity to what amounts to tiny differences in photoperiod. For instance, in some taxa (e.g. European starlings, *Sturnus vulgaris*; Gambel's white-crowned sparrows, *Zonotrichia leucophrys gambelii*), very slight increases in constant photoperiod exposure produce dramatic changes in physiological responses. On constant photoperiods just below 12 L : 12 D, gonads grow slowly and then remain active indefinitely, whereas on exactly 12 L : 12 D photoperiod, oscillating cycles of gonadal activity and inactivity occur, and on photoperiods just above 12 L : 12 D, permanent photorefractoriness follows the initial reproductive development (see Farner *et al.* (1983) and Nicholls

et al. (1988) for reviews). Likewise, male house sparrows on natural photoperiod begin gonadal regression by the time photoperiod has declined less than 30 min after the summer solstice photoperiod of 18 L : 6 D, while others maintained at the summer solstice photoperiod delay onset of regression (Dawson 1991). Thus, even against a background of 18 hours of light per day, at least some temperate zone species are capable of detecting and responding to differences in day length of similar absolute magnitude as tropical species (Hau *et al.* 2000).

The fact that both low- and high-latitude birds possess exquisite sensitivity to small differences in photoperiod illustrates the problem of assuming that differences in the reproductive cue response systems of birds in different environments necessarily represent adaptations. We should be testing the hypothesis that specific features of the cue response systems represent adaptations, not simply searching for evidence that differences exist, and that they appear to be adaptive in the sense of making the birds well suited to those environments. Well suited equals neither 'adapted for' nor 'necessary for' (Ketterson & Nolan 1999). Thus, the intertaxon diversity in different elements of birds' reproductive cue response systems provides the raw material for evaluating whether specific adaptations exist to facilitate appropriate timing of breeding in different environments, but we should use caution when inferring adaptation.

3. EVIDENCE OF ADAPTATION IN REPRODUCTIVE CUE RESPONSE SYSTEMS: HISTORICAL PERSPECTIVE

Although a vast number of experimental studies have been performed on a wide array of avian taxa, comparisons among taxa were hampered from the start by inconsistencies in the experimental approaches used (Farner *et al.* 1983). Nevertheless, illuminating evaluations of the evolutionary significance of differences and similarities among taxa in their cue response systems have been made. Many general reviews discuss differences in cue response patterns and mechanisms that suggest adaptive specialization for different reproductive patterns, especially seasonality versus opportunism (Ball & Hahn 1997; Hahn *et al.* 1997; Dawson *et al.* 2001; Hau 2001; Coppack & Pulido 2004). The most thorough effort to date is still Lofts & Murton's (1968) classic review. They broke photoperiodic taxa into six categories primarily according to experimentally demonstrated differences in photoperiodic thresholds for initial photostimulation, in the degree of tolerance for prolonged exposure to very long days before development of photorefractoriness, and in the subsequent length of the photorefractory period, and discussed how these different features facilitated the different reproductive schedules and migratory patterns displayed, as well as the way that plumage moult was fit into the annual cycle.

Under Lofts & Murton's scenario, Type A species are those with short breeding seasons that begin early in spring but end before the summer solstice (because, from an ultimate standpoint, favourable food supplies and the like have disappeared by then), facilitated by

low thresholds for photostimulation (i.e. below 12 L), and a tendency to develop refractoriness rapidly and maintain it for a long time. This pattern is suitable for sedentary (or only longitudinally migratory), primarily single-brooded taxa living at modest latitudes and exploiting resources that appear for a restricted period of time very seasonally. The examples cited by them include mallards (*Anas platyrhynchos*), European starlings (*S. vulgaris*) and rooks (*Corvus frugilegus*).

Type B species also have a low threshold for photostimulation and, therefore, the capacity to achieve reproductive competence very early in spring, but a high tolerance for long-day exposure without developing refractoriness and a shorter refractory period, leading to a long breeding season that ends well after the summer solstice. This pattern facilitates production of two or more broods, and would be suitable for species exploiting environments where favourable conditions for successful breeding persist longer than for Type A species. Examples include the non-migratory, multi-brooded Nuttall's white-crowned sparrow (*Zonotrichia leucophrys nuttalli*). In both Type A and B species, the fact that the birds remain at mid-latitudes after breeding requires that the refractory period carries far enough into the autumn for short days to prevent reproductive development after refractoriness dissipates, guaranteeing that gonadal recrudescence will not resume until the following winter/spring.

Type C species are those migrating to moderately high latitudes to breed and wintering near the equator where their 'winter' day lengths remain modestly long (e.g. around or somewhat above 12 L : 12 D). A requirement for relatively long photoperiods to induce reproductive competence in spring would help guarantee that they did not achieve full breeding condition until they reached their relatively high-latitude breeding areas. The relatively rapid development of refractoriness, and the long refractory period that ensues in these species, would terminate breeding in time for moult and migration and prevent maladaptive acquisition of breeding condition on the equatorial breeding grounds. Many waders and other equatorial migrants that breed at moderately high northern latitudes were proposed to fall in this category.

Like Type C, Type D species also have a high photostimulation threshold, guaranteeing very late acquisition of breeding condition, but these migratory taxa winter well north of the equator and therefore do not require as long a refractory period as Type C because the day lengths they encounter drop below a fully photosensitive stimulation threshold relatively early in autumn (compared with Type C) and remain short until the following spring. Examples cited include high-latitude breeding subspecies of white-crowned sparrows and juncos—though it is worth noting that the natural refractory period of the taiga-and tundra-breeding Gambel's white-crowned sparrow (*Z. l. gambelii*) extends substantially later into the autumn than suggested would be required for this type of cycle (Farner & Mewaldt 1955).

Type E would be typical of transequatorial migrants that never, or at most briefly, encounter photoperiods less than 12 L : 12 D that prevail as they cross the equator during migration. Birds like the bobolink (*Dolichonyx oryzivorus*) display migratory patterns that match these conditions and possess the expected long threshold for photostimulation, long refractory period and ability to dissipate refractoriness while on relatively long days (Engels 1962).

Type F species are those lacking a refractory period and therefore capable of responding to photostimulation throughout the year. Such species would typically have reproductive schedules symmetrical about the solstices (see Nicholls *et al.* 1988). From the standpoint of the possibility that phylogenetic history may play a role in dictating species' characteristics, it is noteworthy that all of the taxa suggested by Lofts & Murton (1968) to fall into this category are either Columbiformes or Galliformes (mostly quail). It should also be noted, however, that subsequent experimentation with quail has demonstrated that they, in fact, do become refractory, just not absolutely refractory (Robinson & Follett 1982; Nicholls *et al.* 1988; Cockrem 1995; see also Ball & Hahn 1997; Hahn *et al.* 1997; Dawson *et al.* 2001).

Lofts & Murton (1968) also discuss at length the putative adaptations of taxa that presumably do not regulate breeding schedules using photoperiod. They emphasize the importance of responses to non-photic cues such as rainfall and green vegetation, and of the relatively modest temporal changes in gonad size and in spermatogenic status of males compared with photoperiodic temperate zone taxa. Of course, non-photic cues are now well known to be important in highly photoperiodic taxa as well, and are integrated with photoperiod and endogenous annual rhythms for optimal timing of gonadal development, onset of nesting and termination of reproductive competence (see Wingfield *et al.* 1992; Hahn *et al.* 1997).

One of the key points to be taken from Lofts & Murton's (1968) careful analysis is the fact that there are many elements to avian reproductive cue response systems, and these all have the potential to be modified differentially by selection. When considering features of cue responsiveness that would affect the degree to which different taxa are capable of different degrees of temporal reproductive flexibility, Hahn *et al.* (1997) highlighted three general traits that would be highly relevant. First, the minimum photoperiodic threshold ('critical day-length' of Hamner 1968) required for advancement of gonadal development would dictate how early breeding could commence in winter or spring. This feature received extensive attention from Lofts & Murton (1968, see above; see also Hau 2001). Second, the nature of the refractory period (absolute, relative, or absent) would play a fundamental role in determining whether breeding is physiologically possible at different times of a year; taxa displaying only relative refractoriness (reduced, but not completely eliminated, responsiveness to reproductive stimuli) or no refractoriness would be capable of greater temporal flexibility than would be permitted by an absolute refractory period that eliminates responsiveness to all manner of cues (Ball & Hahn 1997; Hahn *et al.* 1997). Third, the extent to which non-photic cues such as food supply, temperature and social interactions can supersede or at least be

Table 1. Summary of cue response characteristics potentially susceptible to natural selection and their suggested significance to reproductive scheduling.

cue response feature	significance
photoperiodic threshold when fully sensitive	affects possible date of earliest onset of breeding
long-day requirement	dictates whether photostimulation is required for gonadal development, or whether non-photic cues might be sufficient under some circumstances
relative sensitivity to photic and non-photic cues	dictates extent to which non-photic cues may induce gonadal development
presence of refractoriness of any kind	determines trade-off of reproductive flexibility and risk of breeding at inopportune times
form of refractoriness (absolute, relative and none)	determines whether any breeding response is possible during refractory phase
duration of refractory period	may determine potential for late summer and autumn breeding attempts
conditions permitting dissipation of refractoriness	dictates whether breeding can only resume after autumn is passed, and whether refractoriness can dissipate on long days on Southern Hemisphere wintering grounds
spontaneous gonadal regression without change in cues	obligate termination of breeding during favourable conditions, guarantees termination of breeding by a certain time; constrains against prolonging breeding
total unresponsiveness to cues during refractory period	dictates obligate hiatus in breeding, even if unusually favourable conditions indicated by non-photic cues were to appear
rate of development of refractoriness	dictates potential duration of breeding season at any particular photoperiod
plasticity of timing of onset of refractoriness depending on non-photic cues	ability to prolong breeding for additional clutches, or when unusual conditions appear late in season, even in absolutely refractory taxa
presence of photoperiod range where reproductive condition is possible but refractoriness does not develop	could permit protracted or continuous breeding at some lower latitudes while producing obligate seasonal breeding at higher latitudes
presence of juvenile refractory period	dictates whether young birds can acquire breeding condition within the same breeding season as they were born

integrated with photic cues (or circannual rhythms) in different species could strongly affect the potential for temporal flexibility of reproduction (see also Wingfield *et al.* 1992, 1993; Hau 2001). Hahn *et al.* (1997) emphasized additional details of the refractory period, in particular, that would affect capacity for reproductive flexibility: (i) timing of onset, (ii) duration, (iii) conditions permitting dissipation, and (iv) the form, absolute or relative. The first three of these were also emphasized by Lofts & Murton (1968), but the existence of relative refractoriness was only reported for the first time, as a transitional stage during dissipation of absolute refractoriness in the house finch, at the time Lofts & Murton's review appeared (Hamner 1968). It was not appreciated to be present as a terminal condition (i.e. present without then proceeding to absolute refractoriness) in Japanese quail for more than another decade (Robinson & Follett 1982). Relative refractoriness is interesting from the standpoint of species' capacity for temporal reproductive flexibility because it facilitates seasonal termination of breeding, as day length declines during summer, without precluding maintenance or resumption of reproductive activity if conditions remain particularly favourable (see Ball & Hahn 1997; Hahn *et al.* 1997; see also below, §5).

Many recent studies have focused especially on photoperiodic threshold as a trait that may be under selective pressure (e.g. Silverin *et al.* 1989, 1993;

Silverin 1995; Lambrechts *et al.* 1996), and although this is perfectly reasonable, we want to emphasize the utility of considering a variety of features of the reproductive cue response system owing to the diverse and important effects they may have on reproductive timing. Table 1 summarizes some features that we feel deserve attention, including all those noted above as well as a few others.

4. ALTERNATIVE EXPLANATIONS: ADAPTIVE SPECIALIZATION, CONDITIONAL PLASTICITY AND PHYLOGENETIC HISTORY

Adaptive specialization of cue response systems could find support from a variety of sources. The most common approach that has been used in the past is to consider data on features of cue response systems in light of the challenges to appropriate reproductive timing (both when to breed, and when not to breed) presented by birds' natural environments (e.g. Lofts & Murton 1968; Farner *et al.* 1983; Hahn *et al.* 1997; Hau 2001). This approach is most convincing when some attempt to consider the possible effects of phylogenetic history is made. Although past reviewers did not explicitly consider the effects of phylogenetic history vis-à-vis Felsenstein (1985), they clearly recognized the potential importance of phylogeny and not just ecology in determining the cue response traits that particular species possess. Based on differences among different groups (e.g. ploceids versus emberizines),

Farner *et al.* (1983) argued that photorefractoriness, which is profoundly important for its effects on timing of termination of breeding and capacity for reproductive flexibility (Farner *et al.* 1983; Nicholls *et al.* 1988; Wilson & Donham 1988; Cockrem 1995; Sharp 1996; Ball & Hahn 1997; Hahn *et al.* 1997; Dawson *et al.* 2001; Hau 2001; Hahn *et al.* 2004; Beebe *et al.* 2005; MacDougall-Shackleton *et al.* 2005), probably has multiple evolutionary origins. Likewise, the evident ease of adaptive specialization of particular features of the photoperiodic response system was argued specifically on the strength of comparisons of very closely related taxa. For instance, whinchat, *Saxicola rubetra*, was categorized as type D (see above) and stonechat, *Saxicola torquata*, as type C. Likewise, Nuttall's white-crowned sparrow (*Z. l. nuttalli*) was categorized as type B and Gambel's white-crowned sparrow (*Z. l. gambelii*) as type D. Nonetheless, the hypothesis that phylogenetic history may dictate cue response character traits was never explicitly enunciated.

Perhaps even more significantly, the possibility that plasticity built into the cue response system might permit appropriate, or perhaps even optimal, timing of the different stages of the annual cycle in diverse environments, without benefit of specialized adaptations to those environments, has received short shrift compared with the plethora of studies reporting adaptive features of the focal species. Photoperiodic response systems are, in fact, beautifully predisposed to permit an array of appropriate responses under different environmental conditions. For instance, within a single taxon, such as Gambel's white-crowned sparrow, there is a nonlinear parametric relationship between day length and rate of gonadal growth from 12 L : 12 D up through 20 L : 4 D, beyond which the growth rate is not further enhanced by longer photoperiods (Farner & Wilson 1957; Farner *et al.* 1981). This suggests that 'photoperiodic drive' on the pituitary by the hypothalamus (cf. Follett & Nicholls 1984; Nicholls *et al.* 1988) increases as photoperiod increases above the minimum stimulation threshold. If, as seems plausible, the total 'reproductive drive' is actually a combination of photoperiodic drive and 'non-photic drive' imposed by other kinds of cues (cf. Hahn *et al.* 1997), then as long as photoperiod is above some minimum threshold to permit other cues to have an effect on the reproductive axis at all (Ball 1993), the drive from stimulatory non-photic cues could act as accelerators (cf. Marshall 1959) to enhance the rate of gonadal development by combining with the drive from photic cues. At very long photoperiods (in this case 20 L : 4D up through constant light; Farner *et al.* 1981), photoperiodic drive would be maximal, thereby leaving little scope for inputs from other cues to affect gonadal condition even if the species is responsive to these types of cues under shorter photoperiods (see Hinde & Steel 1976, 1978; Morton *et al.* 1985; Bentley *et al.* 2000; Lambrechts & Perret 2000). However, on shorter long photoperiods (i.e. above threshold but well below peak photostimulation), where photoperiodic drive is not near maximal, the enhancing effects of non-photic cues could be substantial, potentially bringing individuals up to a rate of gonadal maturation similar to that induced by the longest days. Consequently, the
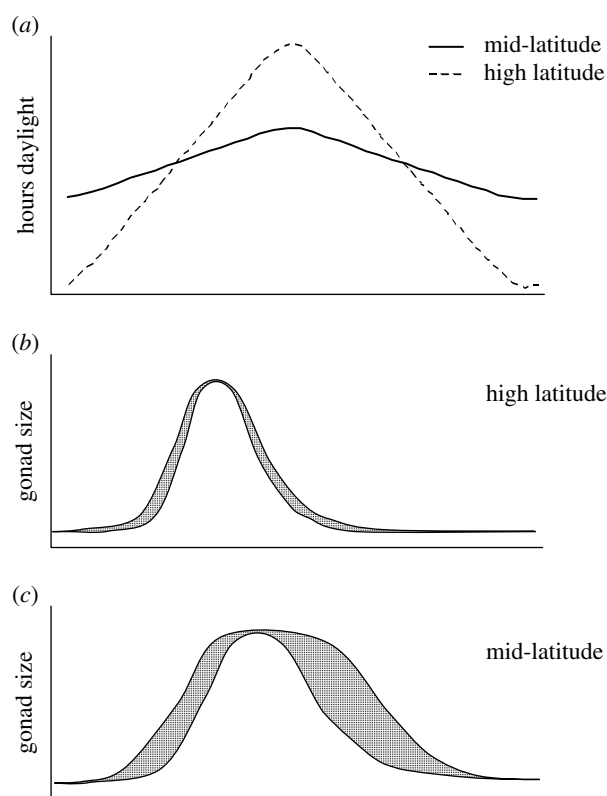
Figure 1. Schematic illustrating conditional plasticity, whereby two birds with identical photoperiod response systems could exhibit different breeding schedules as a result of differing latitude. (*a*) At high latitudes, photophase increases more rapidly in spring, resulting in greater photoperiodic drive: gonads recrudesce more rapidly and refractoriness has an earlier onset. (*b*) Non-photic cues have reduced impact on reproductive flexibility (shaded area) because photoperiod drives the reproductive axis at near-maximal capacity. (*c*) At mid-latitudes photoperiodic drive is reduced: gonads recrudesce more slowly and refractoriness has a later onset. Non-photic cues can have larger impact on onset and offset of breeding.

same individual bird could adjust reproductive schedule adaptively under a range of photoperiodic conditions (illustrated in figure 1). For example, a long and relatively flexible reproductive schedule would naturally emerge if the bird lived at mid-latitudes where photoperiod never gets very long. Flexible timing of acquisition of full reproductive condition in spring would result naturally from only modest photoperiodic drive, with most rapid reproductive development only occurring if non-photic cues were sufficiently favourable to accelerate gonadal maturation. The relatively slow development of absolute photorefractoriness when long days are relatively short (Nicholls *et al.* 1988) inevitably would also contribute to a relatively long breeding season at lower latitudes. In contrast, the same individual bird living at higher latitudes would experience much more vigorous photoperiodic drive under the longer and more rapidly increasing photoperiods of spring, including potentially nearly stepwise increases to very long days if the birds migrate rapidly to high latitudes. This would leave relatively little room for enhancing effects of non-photic cues, which seems appropriate for high-latitude breeders in which gonadal

development happens during migration when the birds are still distant from the actual breeding site, so short-term non-photic cues would not yet be relevant (Wingfield *et al.* 1996). Further, rapid development of refractoriness would terminate breeding relatively quickly. It is also important to keep in mind that non-photic cues, such as social interactions with mates, can specifically influence the timing of onset of photo-refractoriness (e.g. Schwab & Lott 1969; Runfeldt & Wingfield 1985).

The point to be made here is that the same individual bird living in different environments could, by virtue of this *conditional plasticity* built into the cue processing system, generate quite different and highly appropriate reproductive schedules in those different environments. These adaptive breeding schedules need not be the consequence of adaptive specialization to the specific photoperiodic and other cues encountered if the inherent plasticity—which may include the fine-tuning effects of non-photic cues integrated with photoperiod and endogenous rhythms—already copes effectively with the range of variation involved.

Another point of interest is the possibility that early experience programmes individuals, through phenotypic plasticity, to develop reproductive cue response characteristics that are particularly appropriate for the environment occupied. If this is the case, apparent adaptive specializations may, in fact, represent a form of individual plasticity, rather than adaptive specializations to local conditions. The amount of research on this fascinating topic is as yet small in the field of avian reproductive regulation, but there has been significant progress with respect to migratory activity (e.g. Coppack *et al.* 2001), and especially regarding the 'calendar effect' of hatching date on the schedule of plumage moult (see Helm & Gwinner 1999). Several features of the first prebasic (equal to postjuvenal; see Humphrey & Parkes 1959) moult are affected by hatch date, including date of onset and completion, duration and rate (Helm & Gwinner 1999). The response of the first prebasic moult schedule to photoperiodic experience generally leads to adaptive adjustments of moult within the time constraints imposed by birds' environments, but different populations (subspecies) also differ in the degree of responsiveness of the first prebasic moult to photoperiodic influences (Gwinner *et al.* 1983; Helm & Gwinner 1999).

Of course, plastic responses to different environmental conditions may not be adaptive when individuals encounter novel circumstances. Indeed, maladaptive consequences appear to ensue from differences in the relative responsiveness of different elements of the annual cycle to novel photoperiodic conditions (Coppack *et al.* 2001). Blackcaps (*Sylvia atricapilla*) exposed to experimental photoperiods simulating an earlier hatching date did not delay termination of moult and onset of autumnal migratory activity to a degree that would compensate for the simulated advancement of hatching date. This would lead to individuals initiating migration substantially earlier than would be expected to be adaptive, although there is reason to suspect that selection should be able to modify this relationship between hatch date and moult/migration (Coppack *et al.* 2001; see below).

In any case, by being born under different conditions, adjustments in responses to cues could result, some of which at least could be adaptive. This points to the cautionary note that what appears to be adaptive specializations could, in fact, be the result of developmental phenotypic plasticity.

5. CASE STUDY: ABSOLUTE REFRACTORINESS IN SONGBIRDS IN GENERAL, AND CARDUELINE FINCHES IN PARTICULAR

Although reproductive cue response systems function as integrated wholes, it is still instructive to consider particular features alone, since they can have relatively specific effects on the reproductive cycles that are possible, and may be subject to differential selection. Here we will examine one particularly familiar and well-studied phenomenon, the termination of reproductive competence despite the persistence of conditions that should be stimulatory. Changing photoperiod has several important effects on seasonally breeding birds (see Farner & Follett 1979; Farner & Gwinner 1980; Nicholls *et al.* 1988; Wilson & Donham 1988). Lengthening days in spring induce rapid development of the gonads to full reproductive competence. Later, the birds become unresponsive, or *absolutely refractory*, to the stimulatory effects of long days; the gonads regress and the birds become reproductively quiescent despite continued long days. Experimentally, absolute refractoriness has been identified by either of two criteria: (i) gonads spontaneously regress and prebasic plumage moult proceeds without any decline in photoperiod, or (ii) gonadotrophin levels and gonads are unaffected by even longer days (24 L : 0 D in the extreme) once gonads have regressed and moult is advanced (see Hamner 1968; Farner *et al.* 1983; Nicholls *et al.* 1988). During autumn, birds regain photosensitivity and can again respond to long days and other cues (see Farner *et al.* 1983; Nicholls *et al.* 1988; Wilson & Donham 1988; Ball 1993; Sharp 1996; Hahn *et al.* 1997; Ball & Hahn 1997; Wingfield & Farner 1993; Dawson *et al.* 2001). A special form of photorefractoriness, relative refractoriness (see Hamner 1968; Robinson & Follett 1982), reduces but does not eliminate photosensitivity. Species that only become relatively refractory regress gonads on declining summer photoperiod, while days still exceed the spring stimulation threshold, but maintain mature gonads indefinitely on constant long photoperiods, and are still responsive to longer days after declining day length precipitates gonadal regression (Robinson & Follett 1982). Relative photorefractoriness has been best studied in Japanese quail, *Coturnix japonica*, but note that some characteristics of it are present in some other species, such as song sparrows (Wingfield 1993); it may be the only form of refractoriness that crossbills display (Hahn 1995, 1998; Hahn *et al.* 2004). Absolute refractoriness is presumably adaptive in many environments because it completely prevents inappropriately timed late summer and autumn reproductive attempts. It may be costly, however, because it restricts when birds can breed and thus their potential reproductive flexibility. Therefore, it should only evolve, or be maintained, when the cost of missing some legitimate

reproductive opportunities is outweighed by the benefit of not trying to breed at inopportune times. Relative refractoriness confers some of the same advantages as absolute refractoriness by reducing the likelihood of breeding in, for example, late summer and early autumn in largely seasonal environments, but apparently without completely eliminating the possibility of breeding, should unusually favourable conditions be encountered. It therefore seems to be an intuitively superior way to facilitate a seasonal reproductive schedule for species that occasionally encounter conditions that permit successful breeding very late in summer or early autumn (see Hahn *et al.* 1997 for full discussion).

The general question is whether variation in reproductive schedules (seasonal and opportunistic) reflects evolved variation in modulation of responsiveness to cues (sensitivity and refractoriness). The adaptive specialization hypothesis would predict that maximal flexibility (opportunism) requires a persistent high level of responsiveness to environmental cues to permit rapid initiation of breeding whenever unpredictable favourable conditions for breeding are encountered (cf. Farner & Serventy 1960; Ball & Hahn 1997). In contrast, strict seasonality would be facilitated by development of an absolute refractory period that prevents attempted breeding at inappropriate times. Intermediate degrees of flexibility could be facilitated by dissociation of the two absolute refractoriness criteria. Alternatives to the adaptive specialization hypothesis would be that conditional plasticity permits essentially similar cue response systems to produce different adaptive reproductive schedules under different circumstances, or that phylogenetic history explains the distribution of cue response characteristics in different taxa.

We have so far located data regarding absolute refractoriness criterion 1 (spontaneous regression of gonads without a decline in photoperiod) for 41 species of songbirds from seven families (table 2). Of these, only four species (zebra finch, red crossbill, white-winged crossbill and rufous-collared sparrow) failed to regress gonads when held for extended periods on long days (figure 2). All others either regressed spontaneously on constant long photoperiods or regressed gonads while day length was still increasing (table 2). The phylogenetic distribution of failure to meet criterion 1 for absolute refractoriness is consistent with it being a derived trait in the songbirds. Spontaneous gonadal regression definitely appears to be ancestral to the emberizines and fringillines. Among the representatives examined, only the two crossbill taxa in the fringillines and *Zonotrichia capensis* (specifically, the subtropical form, *Z. c. hypoleuca,* was studied; it will be interesting to see whether higher-latitude subspecies of this widely distributed taxon are similar to *Z. c. hypoleuca*) among the emberizines fail to display the trait. This distribution of the trait supports the loss of refractoriness criterion 1 representing an adaptive specialization for greater reproductive flexibility. Zebra finches (*Taeniopygia guttata*) and crossbills (*Loxia curvirostra* and *Loxia leucoptera*) are archetypal opportunists that have been proposed to possess features that facilitate temporal reproductive plasticity

(see Hahn *et al.* 1997 for review; see also Perfito *et al.* 2006). Rufous-collared sparrow (and particularly *Z. c. hypoleuca*) is the sole tropical and subtropical representative of its genus (though its geographical range extends well into the south temperate zone as well), and these birds display a long flexible reproductive schedule (see Moore *et al.* 2004). All other taxa represented in figure 1 qualify as seasonal breeders with the exception of *Quelea*. It is noteworthy that although quelea do spontaneously regress their gonads when held on constant long days, they also rapidly dissipate refractoriness and reattain reproductive condition without a short-day requirement (Lofts & Murton 1968). This ability may be widespread in the Passeridae: at least some individual house sparrows (*Passer domesticus*) also can dissipate absolute refractoriness when continuously exposed to long days (see Farner *et al.* 1983; see also Hahn *et al.* 1997), and it may facilitate substantial reproductive plasticity in the group. Some other taxa (e.g. song sparrows, *Melospiza melodia melodia*; Wingfield 1993) also display this characteristic, at least in some individuals; it will be illuminating to determine how this trait is distributed among a wider array of taxa.

The *Zonotrichia* warrant additional comment. All four congeners of *Z. capensis* (*Zonotrichia leucophrys*, *Zonotrichia atricapilla*, *Zonotrichia albicollis* and *Zonotrichia querula*) winter in the north temperate zone, breed at temperate, subarctic and Arctic latitudes, and spontaneously regress gonads when held on constant long days. *Z. capensis* has been shown by a variety of phylogenetic methods to be the most basal lineage in the genus (Zink 1982; Zink *et al.* 1991; Zink & Blackwell 1996; Patten & Fugate 1998). Thus, the overall distribution of absolute refractoriness criterion 1 within *Zonotrichia* and among near out-groups (*Melospiza*, *Junco* and *Spizella*) suggests that this trait was lost as an adaptive specialization to breeding at low latitudes along the lineage leading directly to *Z. capensis*, but retained as an ancestral trait in the lineage leading to all other *Zonotrichia*. Other possible explanations (e.g. loss of absolute refractoriness criterion 1 along the lineage from other emberizines to the genus *Zonotrichia*, followed by reappearance of refractoriness criterion 1 at the branch point uniting *Z. capensis* to the rest of the genus) require more evolutionary events and are therefore less parsimonious.

Data on refractoriness criterion 1 are particularly interesting when examined in more detail within the cardueline finches. Cardueline finches are ideal for testing the relationships among reproductive schedule and cue responsiveness modulation (refractoriness, according to both criterion 1, spontaneous termination of reproductive competence without a decline in day length, and criterion 2, complete unresponsiveness to long days). They are a diverse tribe (Carduelini) in the family Fringillidae (Sibley & Monroe 1990), and they range from seasonal to opportunistic breeders. Reproductive schedules of many are restricted to late spring and early summer (e.g. Hahn 1996; MacDougall-Shackleton *et al.* 2000), but crossbills (opportunists) regularly breed January–September and occasionally in any month if the conifer seeds on which they specialize are sufficiently abundant (Benkman 1990, 1992;

Table 2. Distribution of photorefractoriness, defined by criterion 1 (spontaneous regression of gonads while on constant stimulatory long days) among songbird species. Taxonomy follows Sibley & Ahlquist (1990) and Monroe & Sibley (1993).

common name	latin name	refractory?	conditions/comments	citation
family Corvidae				
black-billed magpie	*Pica pica*	yes	natural (gonads regress while day length is still increasing in spring)	Erpino (1969)
rook	*Corvus frugilegus*	yes	natural (gonads regress while day length is still increasing in spring)	Marshall & Coombs (1957)
family Muscicapidae subfamily Turdinae				
European blackbird	*Turdus merula*	yes	natural (gonads began regression before photoperiod declined, both sexes)	Partecke *et al.* (2004)
subfamily Muscicapinae tribe Saxicolini				
stonechat	*Saxicola torquata*	yes	increasing (gonads regressed while days still increasing)	Helm & Gwinner (2005)
family Sturnidae				
European starling	*Sturnus vulgaris*	yes	15 L : 9 D	Burger (1947)
Brahminy myna	*Sturnus pagodarum*	yes	12 L : 12 D 14 L : 10 D 16 L : 8 D both sexes tested	Kumar & Kumar (1993)
Common myna	*Acridotheres tristis*	yes	15 L : 9 D	Chaturvedi & Thapliyal (1983)
family Paridae				
willow tit	*Parus montanus*	yes	20 L : 4 D	Silverin & Viebke (1994)
black-capped chickadee	*Parus (Poecile) atricapillus*	yes	15 L : 9 D	Phillmore *et al.* (2005)
great tit	*Parus major*	yes	increasing (testes regressed while pp still increasing) 20 L : 4 D (regressed completely)	Silverin *et al.* (1993); Silverin & Viebke (1994)
family Sylviidae				
garden warbler	*Sylvia borin*	yes	15 L : 9 D	Gwinner *et al.* (1988)
family Passeridae subfamily Passerinae				
house sparrow	*Passer domesticus*	yes	18 L : 6 D 16 L : 8 D	Dawson (1991); Hahn & Ball (1995)
chestnut-shouldered petronia	*Petronia xanthocollis*	yes	15 L : 9 D	Tewary & Tripathi (1985)
subfamily Ploceinae				
common (Baya) weaver	*Ploceus philippinus*	yes	13 L : 11 D; 14 L : 10 D but does not regress on 15 L : 9 D (held 15 months)	Thapliyal & Saxena (1964); Chandola & Chakravorty (1982); Chakravorty & Chandola-Saklani (1985)
red-billed quelea	*Quelea quelea*	yes	12 L : 12 D; 17 L : 7 D	Lofts (1962, 1964)
subfamily Estrildinae				
zebra finch	*Taeniopygia guttata*	no	17 L : 7 D and 9 L : 15 D for eight months, with and without water, no gonadal differences among groups...all big at end.	Sossinka (1974)
spotted munia	*Lonchura punctulata*	yes	24 L : 0 D	Chandola-Saklani *et al.* (2004)
family Fringillidae subfamily Fringillinae tribe Fringillini				
chaffinch	*Fringilla coelebs*	yes	uncertain (long days)	Dolnik, (1975, 1976*a,b*; cited in Farner *et al.* (1983))
tribe Carduelini				
white-winged crossbill	*Loxia leucoptera*	no	20 L : 4 D gonads did regress slightly but significantly after five months, but were still breeding size	Hahn *et al.* (2004)
red crossbill	*Loxia curvirostra*	no	16 L : 8 D (Groth's (1993) type 2 and type 3)	Hahn (1995), unpublished

(*Continued.*)

Table 2. (*Continued.*)

common name	latin name	refractory?	conditions/comments	citation
common redpoll	*Carduelis flammea*	yes	20 L : 4 D	Hahn *et al.* (2004)
pine siskin	*Carduelis pinus*	yes	20 L : 4 D	Hahn *et al.* (2004)
American goldfinch	*Carduelis tristis*	yes	18 L : 6 D both males and females	Marsh *et al.* (2002)
greenfinch	*Carduelis chloris*	yes	16 L : 8 D, based on only a single individual	Damste, (Damsté 1947)
canary	*Serinus canaria*	yes	20 L : 4 D; 16 L : 8 D. did not regress on 11 L	Storey & Nicholls (1976)
house finch	*Carpodacus mexicanus*	yes	18 L : 6 D; 12 L : 12 D; results a bit more ambiguous on 10 L : 14 D but regression did occur	Hamner (1966)
Cassin's finch	*Carpodacus cassinii*	yes	15 L : 9 D; based on completion of normal moult and regression of cloacal protuberances	Hahn unpublished
common rose-finch	*Carpodacus erythrinus*	yes	15 L : 9 D; 24 L : 0 D both males and females spontaneously regress on 15 L : 9 D	Kumar & Tewary (1982); Tewary & Dixit (1983), Tewary *et al.* (1983)
eurasian bullfinch	*Pyrrhula pyrrhula*	yes	16 L : 8 D	Storey & Nicholls (1982)
subfamily Emberizinae tribe Emberizini				
black-headed bunting	*Emberiza melanocephala*	yes	11.5 L : 12.5 D; 12 L : 12 D; 12.5 L : 11.5 D; 13 L : 11 D; 15 L : 9 D all spontaneously regressed	Tewary & Kumar (1982); Misra *et al.* (2004)
red-headed bunting	*Emberiza bruniceps*	yes	12 L : 12 D; 12.25 L : 11.75 D; 12.5 L : 11.5 D; 13 L : 11 D; 14 L : 10 D; 18 L : 6 D all spontaneously regressed (11.5 and 11.75 L did not)	Rani *et al.* (2005*b*)
Lapland longspur	*Calcarius lapponicus*	yes	23 L : 1 D	Hunt & Wingfield, unpublished (personal communication)
song sparrow	*Melospiza melodia*	yes	18 L : 6 D	Wingfield (1993)
rufous-collared sparrow	*Zonotrichia capensis*	no	20 L : 4 D (300 + days without regression) 10 L : 14 D	Lewis *et al.* (1974)
harris' sparrow	*Zonotrichia querula*	yes	20 L : 4 D	Donham & Wilson (1970)
white-throated sparrow	*Zonotrichia albicollis*	yes	13 L : 11 D; 20 L : 4 D	Harris & Turek (1982)
white-crowned sparrow	*Zonotrichia leucophrys*	yes	16 L : 8 D; 18 L : 6 D; 20 L : 4 D; 22 L : 2 D; 23 L : 1 D; 23.5 L : 0.5 D; 24 L : 0 D	Moore *et al.* (1982); Farner *et al.* (1983)
golden-crowned sparrow	*Zonotrichia atricapilla*	yes	20 L : 4 D	Wingfield, unpublished (2002, personal communication)
dark-eyed junco	*Junco hyemalis*	yes	20 L : 4 D	Wolfson (1952); Wolfson (1959)
American tree sparrow	*Spizella arborea*	yes	20 L : 4 D (both sexes tested)	Wilson & Follett (1974)
tribe Icterini				
Bobolink	*Dolichonyx oryzivorus*	yes	14 L : 10 D	Engels (1959)

Adkisson 1996). We have sufficient data within cardue-lines to perform informative analyses of the distribution of both refractoriness criteria 1 and 2. House finches (*Carpodacus mexicanus*), Cassin's finches (*Carpodacus cassinii*), scarlet rose-finches (*Carpodacus erythrinus*) and grey-crowned rosy-finches (*Leucosticte tephrocotis*) are all seasonal breeders. Wild populations of canaries (*Serinus canaria*) have a flexible breeding schedule (Leitner *et al.* 2003). American goldfinches (*Carduelis tristis*), pine siskins (*C. pinus*), common redpolls (*Carpodacus flammea*), red crossbills (*L. curvirostra*) and white-winged crossbills (*L. leucoptera*) represent a speciose group of recently evolved close relatives (Marten & Johnson 1986; Arnaiz-Villena *et al.* 2001). Redpolls and goldfinches breed seasonally. Siskins are flexible, breeding from early spring through late summer if food is sufficiently abundant (Hahn, unpublished observations). Although fundamentally seasonal (Dawson 1997), siskins are capable of arresting plumage moult and resuming breeding in mid-summer,
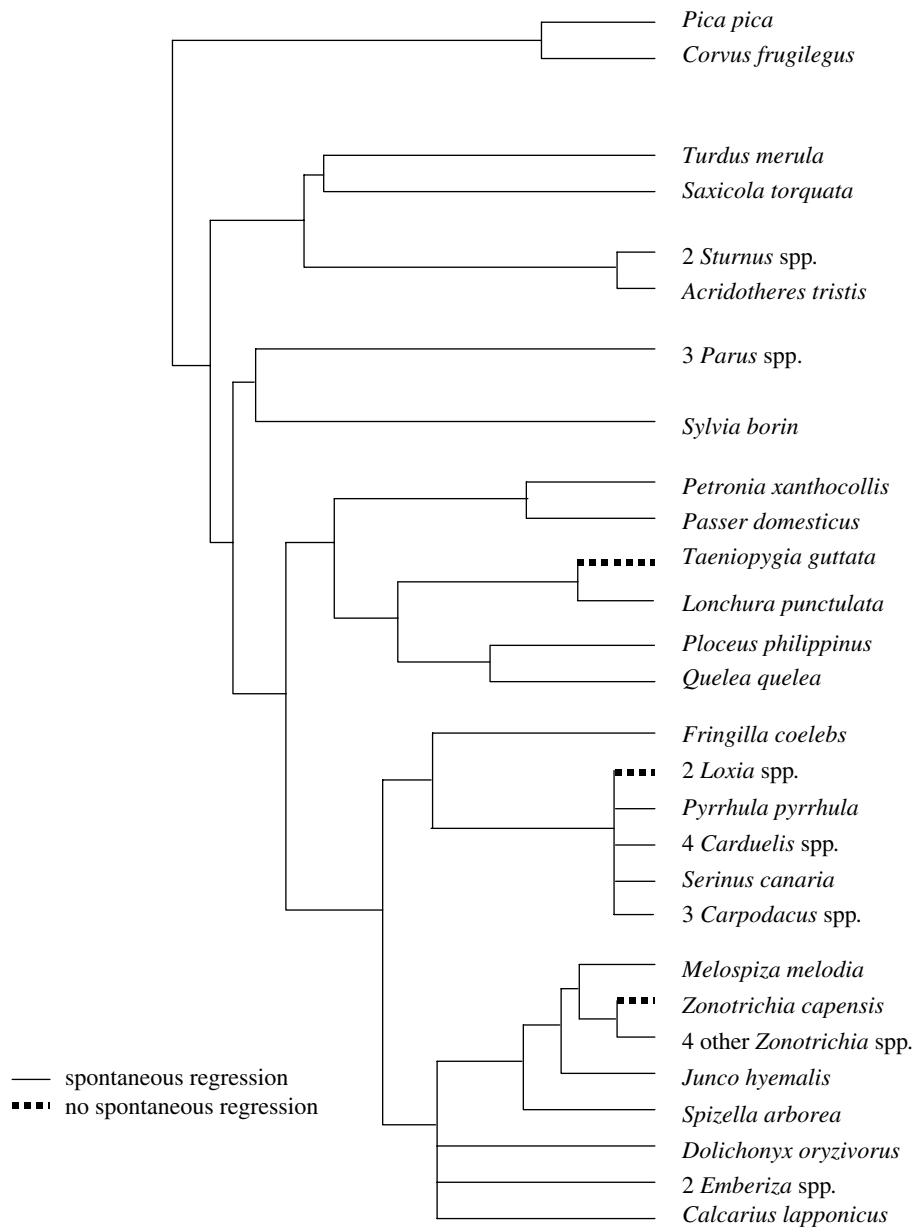
Figure 2. Distribution of absolute refractoriness defined by criterion 1 (spontaneous regression of gonads on constant long days). Phylogeny adapted from Sibley & Ahlquist (1990), based on DNA–DNA hybridization. Higher-order taxa, common names of taxa and references in table 2.

after the normal spring breeding has ended (Hahn 1992, unpublished data). Bullfinches (*Pyrrhula pyrrhula*) resemble pine siskins in displaying a flexible seasonal breeding schedule that appears to be capable of substantial extension in late summer if preferred foods are particularly abundant (Newton 1973). Crossbills are the most flexible, breeding at least occasionally in any month, on any naturally occurring mid-latitude photoperiod if food (conifer seeds) is abundant (Benkman 1990, 1992; Hahn 1995, 1998; Adkisson 1996). Many field-caught crossbills show clear evidence of arrested moult (indicative of reversal of reproductive regression after spring breeding; Hahn *et al.* 1992) when breeding in late summer (Hahn 1998 and unpublished).

Within carduelines, refractoriness criterion 1 data are, so far, clear-cut (table 2, figure 2). Both crossbill species fail to regress gonads on constant long days. All other carduelines tested, including flexibly seasonal taxa such as canaries, pine siskins and bullfinches

(Newton 1973; Storey & Nicholls 1976; Bentley *et al.* 2003; Hahn *et al.* 2004), do spontaneously regress gonads on constant long days. It is worth noting that this regression may take an extended period of time in these flexible breeders—up to 50 weeks in bullfinches (Storey & Nicholls 1982). However, all seasonally breeding carduelines tested thus far, whether flexible or strictly seasonal, display refractoriness as defined by criterion 1. Conditional plasticity may account for apparent differences in the time taken by some flexible taxa take to become refractory: the bullfinches were tested on 16 L : 8 D photoperiod (Storey & Nicholls 1982) while the pine siskins were tested on 20 L : 4 D photoperiod, which is well known to drive birds through to refractoriness sooner than shorter long days (Nicholls *et al.* 1988). Thus, within carduelines, loss of spontaneous gonadal regression appears to represent a recent, and intuitively sensible, adaptive specialization unique to the opportunistic crossbills,

facilitating continued late-season breeding if food supply permits.

Fewer cardueline taxa have been tested for absolute refractoriness criterion 2 (lack of response to 24 L after gonadal regression). Different character states for this trait could be complete lack of response when challenged, delayed response or immediate and sustained response. Immediate and sustained response would facilitate maximum flexibility (opportunism), but a delayed response (e.g. if gonadotrophin-releasing hormone production needed to be reinitiated first; see Ball & Hahn 1997; Hahn *et al.* 1997) would permit flexibility. Of the seven cardueline taxa that have been tested for this trait, only the three *Carpodacus* (house finch, Cassin's finch and scarlet rose-finch) show no response (MacDougall-Shackleton *et al.* 2005). This sandwiches total unresponsiveness between responsiveness in the more basally derived rosy-finch (*Leucosticte*) and that in the rest of the species. Had the rosy-finches displayed unresponsiveness, like the *Carpodacus*, this would have supported the interpretation that total unresponsiveness evolved after *Carpodacus* diverged from the main cardueline lineage. All of the cardueline genera that evolved after the *Carpodacus* branch contain at least some highly flexible species, so this result would have supported adaptive specialization through reappearance of responsiveness after gonadal regression. However, the fact that rosy-finches are responsive to 24 L after gonadal collapse suggests the alternative possibility that responsiveness appeared (having been absent in taxa ancestral to the carduelines) early in the cardueline lineage and has been retained in many carduelines through phylogenetic descent, only having been lost in *Carpodacus*, perhaps as an adaptive specialization for seasonal breeding, which may be universal in that largely Old World genus. Under this scenario, response to 24 L challenge after gonadal regression (i.e. lack of real absolute refractoriness; see Hamner 1968) would exist as an ancestral character that predisposed many recently evolved carduelines to be capable of flexible reproductive schedules, but it would not represent a derived adaptive specialization for that function in those taxa. Thus, with respect to refractoriness criterion 2, there is currently provisional support for both adaptive specialization (*Carpodacus* re-evolving unresponsiveness to facilitate seasonal breeding) and phylogenetic history (all other taxa having inherited from an early cardueline ancestor an ability to respond to long days, and possibly other cues, after gonads regress). Thorough study of rosy-finches (*Leucosticte*) and other more basally derived taxa (pine grosbeak, *Pinicola enucleator,* and evening grosbeak, *Coccothraustes vespertinus*, would be good choices) is required before this interpretation can be confirmed.

Overall, the clearest support for adaptive specialization comes from the crossbills. Of all the cardueline taxa tested this far, they alone maintain active gonads indefinitely on constant long days and also remain responsive to 24 L even after the gonads regress. Interestingly, they also differ from most other songbirds studied to date in failing to show seasonal downregulation of the hypothalamic gonadotrophin-releasing hormone (GnRH) system that regulates activity of the pituitary and gonads (MacDougall-Shackleton *et al.* 2001; Pereyra *et al.* 2005; for general discussions of the functional significance of seasonal downregulation of the GnRH system, see Ball & Hahn 1997; Hahn *et al.* 1997; Dawson *et al.* 2001; MacDougall-Shackleton *et al.* 2005). They are also the only carduelines known to be able to breed on any naturally occurring temperate zone photoperiod. The fact that the crossbills' closest relatives, the redpolls, are seasonal breeders that spontaneously regress the gonads on constant long days (and downregulate the GnRH system, Pereyra *et al.* 2005) strongly reinforces the interpretation that crossbills have evolved specialized cue response system adaptations which facilitate temporal reproductive flexibility, rather than that crossbills' traits are simply inherited from ancestors (phylogenetic history) or that all carduelines are basically similar and capable of similar degrees of reproductive flexibility depending on local photic and non-photic conditions (conditional plasticity).

6. IMPLICATIONS FOR EVOLUTION, INVASION OF NEW HABITATS AND EFFECTS OF CLIMATE CHANGE

The recent excellent review by Coppack & Pulido (2004) regarding the implications of cue response (particularly photoperiodic) patterns and mechanisms for evolution, invasion of novel habitats or geographical areas and effects of climate change on bird populations obviates our going into great detail on the topic here. Consequently, we will be brief and focus mostly on ways in which the ideas we present here augment or, in some cases, deviate from their thoughts.

It is evident from the prevalence of references to adaptive significance of the features of cue response mechanisms observed in different studies (in practically every paper we have read on physiological responses to reproductive cues) that it is generally assumed that cue response systems are responsive to selection. The belief in adaptive adjustment of cue response systems is apparent in Farner *et al.*'s (1983) suggestion that photorefractoriness has multiple evolutionary origins within birds. Lofts & Murton (1968) are very explicit that they think cue response systems must evolve relatively easily owing to apparent adaptive specializations in close relatives, e.g. within the genera *Saxicola* and *Zonotrichia*. They also describe what they consider to be the relative ease with which the photoperiodic system of a tropical species like *Quelea quelea* could be modified by selection to match that of a temperate zone species like *Passer domesticus*. It is clear, however, that some key elements of the natural house sparrow reproductive pattern, such as accelerated termination of breeding on very long days, would emerge naturally from the conditional plasticity already present in *Quelea* (Lofts & Murton 1968). Common-garden experiments with different populations of blue tits (*Parus caeruleus*) and great tits (*P. major*) have now shown that local adaptation of the photoperiodic response systems of tits has occurred not only in populations at dramatically different latitudes (cf. Silverin *et al.* 1989, 1993; Silverin 1995), but is evident in geographically very close populations that normally experience similar photoperiods but occupy areas

where timing of changes in food supply favour different reproductive schedules. Differential responses to non-photic environmental cues, such as also exist in different tit species (Silverin & Viebke 1994), are not required to explain the observed differences in egg-laying dates under experimental conditions (Lambrechts *et al.* 1996, 1997). This finding is of particular interest because it demonstrates an evolved adjustment of photoperiodic response patterns in a situation that would have been historically suspected to involve only responses to non-photic cues, i.e. fine-tuning of the photically controlled schedule (see Wingfield *et al.* 1992; Lambrechts *et al.* 1996).

Although adaptation may occur readily, the most recent research on this topic reveals that it does not necessarily do so. Under apparent selection for earlier onset of breeding as climate warms and peak food abundance advances, at least one population of great tits (*Parus major*) in the Netherlands has failed to show any adaptive advancement of laying date, apparently owing to a mismatch between the cues that the tits have evolved to use (primarily photoperiod) and the pattern of appearance of the ultimate factor under a changing climate (Visser *et al.* 1998, 2004). Most pertinent to our own discussion above is the idea that photoperiodic response patterns may either constrain or enhance adaptation to novel environments, depending on whether the inherent plasticity in the response system leads to adaptive or maladaptive suites of changes in the annual cycle in the short term. If the plastic (within individuals) responses are adaptive, then facilitation or reinforcement of further (genetically based) adaptation to the new conditions may occur (Coppack & Pulido 2004). In this context, it becomes particularly important to consider how novel environmental conditions might affect a suite of characteristics of the cue response system, such as those presented in table 1, rather than just one. Consideration of multiple elements of the environmental cue response system may, like consideration of different elements of the annual cycle (e.g. breeding, moult, migration), help to reveal whether failure to show an adaptive response in one component is constrained by obligations dictated by another element. In the comparative analysis we present here, we consider only one (songbirds generally) or two (carduelines) elements of the cue response system. The potential for constraints of one component on others owing to the entire syndrome of responses, and the question of whether effects of one element on others can be decoupled under selection, is clearly important to both the potential for adaptation to new environments and the response to global climate changes. In this regard, it is noteworthy that the two criteria that are generally used to identify absolute photorefractoriness apparently have been decoupled in several cardueline taxa (figure 3; see MacDougall-Shackleton *et al.* 2005). Clearly these should not be considered equivalent, but rather should be treated as separate elements of cue response systems.

When considering the interplay between adaptive specialization and conditional plasticity, it becomes critical to perform studies that facilitate characterization of reaction norms. The ideal approach of measuring the responses of individuals to a range of conditions would clearly be challenging, perhaps impossible, given the time it takes to perform cue response experiments as well as the possibility that exposure of an individual to one set of experimental circumstances might affect how it responds to other conditions tested subsequently. Even the powerful alternative split sibling approach (e.g. Helm & Gwinner 1999; Coppack *et al.* 2003) is challenging, requiring access to substantial numbers of captive-raised young. Still, population level estimates of reaction norms (see van Noordwijk 1990; Stearns 1992; Helm & Gwinner 1999) can give an idea of the range of responses possible, and thereby a sense of the extent to which plasticity of responses to particular patterns of environmental cues is likely to be adaptive or not. In this context, the biggest concern may be the possibility that cue responses measured in any given individual have been determined substantially by the environment (e.g. latitude=photoperiod) at which it was born and developed.

It may be the reaction norm, rather than any particular response to a particular set of circumstances, that is under selection (see Visser & Lambrechts 1999). The question of how selection operates on reaction norms remains unresolved (see Coppack *et al.* 2001), and is of particular interest when contemplating how extremely flexible species, individuals of which may breed under dramatically different conditions in different years, will be affected by selection. Individual crossbills evidently breed on both the shortest and longest days of the year at specific locations. For instance, several individual male red crossbills (Groth's 'Type 2', one of the largest North American forms; Groth 1993) had breeding-size testes when captured in August 1988 in Central Washington State, and likewise had fully enlarged testes again when recaptured at the same site in January 1989 (population confirmed to be breeding at both times by capture of ovulating and incubating females, and by timing of appearance of dependent young; Hahn unpublished; Coombs-Hahn 1993). Further, as nomads, individual crossbills can breed at dramatically different latitudes in different years. Crossbills of the smallest North American form (Groth's 'Type 3'; Groth 1993) commonly occur from northern California to coastal Alaska (a range of approx. 40°–60° N latitude), and individual birds probably breed at very different latitudes in different years. For instance, an adult female that we banded on the Olympic Peninsula of Washington State (47° N latitude) near the end of summer breeding in 2003 was subsequently recovered, and probably had bred in summer, near Juneau, Alaska (58° N latitude) 2 years later (Hahn, unpublished). Both the flexible reproductive timing and nomadism can thus lead to substantial, even extreme, variation in the conditions under which nestlings are raised; summer solstice photoperiod in northern California and southeast Alaska differs by approximately 3 hours (15 L : 9 D versus 18 L : 6 D), and photoperiods in January and July in the Washington Cascade Mountains differ by approximately 8 hours (8 L : 16 D versus 16 L : 8 D). In cases like this, local adaptation to particular photoperiodic and other environmental features clearly would be at best useless and at worst counter productive. In such cases, a system
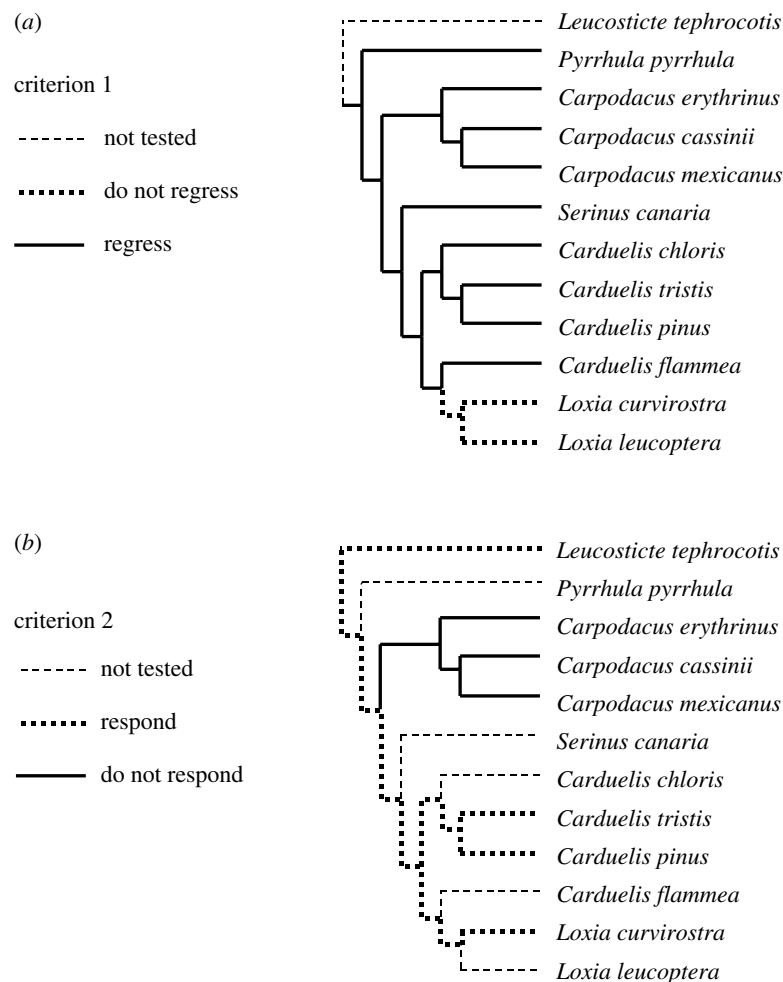
(a)

criterion 1

‑ ‑ ‑ ‑ ‑ ‑   not tested

·········   do not regress

————   regress

- *Leucosticte tephrocotis*
- *Pyrrhula pyrrhula*
- *Carpodacus erythrinus*
- *Carpodacus cassinii*
- *Carpodacus mexicanus*
- *Serinus canaria*
- *Carduelis chloris*
- *Carduelis tristis*
- *Carduelis pinus*
- *Carduelis flammea*
- *Loxia curvirostra*
- *Loxia leucoptera*

(b)

criterion 2

‑ ‑ ‑ ‑ ‑ ‑   not tested

·········   respond

————   do not respond

- *Leucosticte tephrocotis*
- *Pyrrhula pyrrhula*
- *Carpodacus erythrinus*
- *Carpodacus cassinii*
- *Carpodacus mexicanus*
- *Serinus canaria*
- *Carduelis chloris*
- *Carduelis tristis*
- *Carduelis pinus*
- *Carduelis flammea*
- *Loxia curvirostra*
- *Loxia leucoptera*

Figure 3. Distribution of two criteria for absolute photorefractoriness among cardueline finches. (*a*) Criterion 1 is spontaneous gonadal regression while on constant long days. (*b*) Criterion 2 is unresponsiveness to long days (24 hour light in the extreme) during photorefractoriness. Common names of taxa and references in table 2. Phylogeny adapted from Marten & Johnson (1986), Badyaev (1997) and Arnaiz-Villena *et al*. (2001).

with suitably plastic photoperiodic responses (crossbills are definitely photoperiodic; Tordoff & Dawson 1965; Hahn 1995) would be essential, but given the potential for responses of one feature of the annual cycle to constrain modification of responses in others (e.g. timing of breeding onset versus moult completion versus migratory onset; see Coppack *et al*. 2001), the precise nature of the plasticity that would be favoured is not yet clear. It also seems sensible to consider carefully the effect that interannual variation in conditions at particular sites, leading to substantial differences in optimal breeding timing among years, might have on the reaction norms which are favoured by selection.

In closing this section, we wish to emphasize two additional things: First, it is probably not possible to overestimate the importance—thoroughly appreciated already by the researchers who have been studying integration of annual cycles of moult, migration and reproduction in stonechats and old world warblers (Gwinner, Berthold and colleagues), as well as by several Indian researchers (Chandola-Saklani, Kumar and colleagues), and several of the pioneers in photoperiodism studies (e.g. Alden Miller, Donald Farner, Albert Wolfson, William Hamner)—of characterizing cue responsiveness characteristics of taxa across a range of stimulus values (e.g. photoperiodic

treatments and the like), rather than simply making comparisons among taxa under a single set of photoperiodic circumstances. Although simple common garden experiments under a single set of conditions are certainly informative, they fail to capture how cue response systems of different taxa vary in their potential outputs under different conditions (i.e. conditional plasticity). Clearly, obtaining some indication at least of mean population reaction norms (see also van Noordwijk 1990; Stearns 1992; see Helm & Gwinner 1999) gives a much clearer idea of how cue responsiveness differs among taxa, of the possibility that adaptive specialization has occurred, and of how conditional plasticity differences among taxa may affect behaviour in different environments. Performing experiments across a range of conditions also has somewhat more mundane advantage of simply reducing the likelihood of misclassification of taxa into particular trait categories. In our analysis, for instance, the original paper describing the response of the Baya weaver (*Ploceus philippinus*) to long days used a single long-day photoperiod treatment, 15 L : 9 D (Thapliyal & Saxena 1964), and reported no spontaneous regression of the gonads even after 15 months of exposure. Subsequent studies testing a range of photoperiods (Chandola & Chakravorty 1982;

Chakravorty & Chandola-Saklani 1985) not only produced results on 15 L : 9 D identical to Thapliyal and Saxena's findings, but also demonstrated that complete spontaneous regression did occur on some other long-day photoperiods (e.g. 13 L : 11 D and 14 L : 10 D), and partial spontaneous regression occurs on 16 L : 8 D (Rani *et al.* 2005*a*).

Second, keeping clearly in mind the strengths and limitations of comparative approaches and attempting to establish perspectives at multiple comparative scales are extremely important. Detailed comparative studies of closely related taxa, such as the stonechats (see Helm *et al.* 2005 for review) and North American *Zonotrichia* (Lofts & Murton 1968; see also reviews by Farner *et al.* 1983; see Wingfield *et al.* 1996, 1997, 2003) are extremely powerful but can lead to misinterpretations if one does not step back to a slightly broader comparative perspective as well. For instance, failure to consider the prevalence of absolute refractoriness within songbirds generally could easily lead to the misconception that because *Zonotrichia capensis hypoleuca* is the most basally derived lineage among *Zonotrichia* (see above), its character state of no absolute refractoriness is therefore likely to represent the ancestral condition within the genus. In light of broader comparative data (figure 2), it is much more likely that *Z. capensis* (at least the tropical forms of *Z. capensis*) evolved a novelty in losing absolute refractoriness, whereas the remainder of the *Zonotrichia* lineage retained the ancestral refractoriness trait. Indeed, it will be useful to consider photoresponsiveness of songbirds in relation to other orders of birds that display phenomena such as relative refractoriness, but a comparative analysis at this level is beyond the scope of our current review.

7. SUMMARY AND SYNTHESIS

In this paper, we combine a comparative approach with explicit enunciation of three hypotheses—adaptive specialization, conditional plasticity and phylogenetic history—to examine adaptation of environmental cue response systems regulating reproductive timing in birds. The analysis within songbirds, in general, and cardueline finches, in particular, provides evidence for contributions of both phylogenetic history and adaptive specialization of these systems. We also present and discuss evidence of conditional plasticity that is probably present in all taxa to differing degrees. We suggest that the degree to which this plasticity is present in different taxa is of substantial significance to trade-offs and constraints affecting those taxa with respect to colonizing new habitats or adjusting (within individuals) or adapting (within populations) to ongoing changes in currently occupied habitats.

Conditional plasticity of photoperiod response systems has often been tacitly excluded from consideration in many previous studies. Characterizing inherent conditional plasticity would ideally use a reaction norm approach (see, e.g. Helm & Gwinner 1999), but, more practically, should at least compare taxon-level variation in responses across a range of cue values, such as maximum day length or rate of change of day length.

Perhaps one of the most illuminating undertakings for future research would be to expand and extend to additional taxa the types of detailed evaluations of numerous environmental cue response system features (a non-exhaustive list of promising features listed in table 1) that have so far been made in only a few taxa. Careful selection of these additional taxa based on their specific reproductive and migratory biology as well as their phylogenetic positions is important to maximize the meaningful insights these further studies will probably yield. For instance, it should be particularly illuminating to characterize in detail the cue response systems, including inherent conditional plasticity, of a few taxa whose phylogenetic relationships are well understood that differ in degree of nomadism versus site fidelity. Since site-faithful taxa would presumably be in situations more conducive to local adaptation (e.g. of photoperiodic cue response characteristics, or tendency to integrate non-photic cues such as food availability; see Lambrechts *et al.* 1996, 1997; see also Schoech & Hahn submitted) than would nomads, such comparisons may help to reveal more clearly the factors favouring, and trade-offs involved in, adaptive specialization optimizing reproductive performance in specific habitats (or locations) as opposed to conditional plasticity permitting adequate reproductive performance across a range of habitats (or locations). We concur with Helm *et al.* (2005) that continued experimentation in a comparative context is vital and certain to provide useful insight into the capacity of birds to adjust to a changing environment.

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