

Phenology

False estimates of the advance of spring

Bias is introduced into almost all recent reports of climate-related trends in the phenology of spring events (for example, the timing of migration, egg laying and ice melt) by giving the calendar date of such occurrences each year, rather than their timing relative to the vernal equinox (refs 1–8, but see ref. 9). Most of these studies overestimate the advance of spring events, as the calendar date of the vernal equinox shows a trend to become earlier throughout any century, although this bias is small in the examples published so far. However, its magnitude cannot be predicted for any data set that is extended into the twenty-first century, because of long-term changes in the date of the vernal equinox. As phenological data are important for studying climate change, trends need to be reported in terms that accurately reflect changes to the Earth system.

Trends in the calendar date of the vernal equinox within centuries arise from the discrepancy between our average 365.25-day calendar (accounting for leap years) and the roughly 365.2422-day ‘vernal equinox year’ (the average time between successive vernal equinoxes). This difference causes the equinox to arrive about 0.78 days earlier on the calendar over 100 years (Fig. 1a). Because years that are divisible by 100 (but not by 400) are not leap years¹⁰, trends

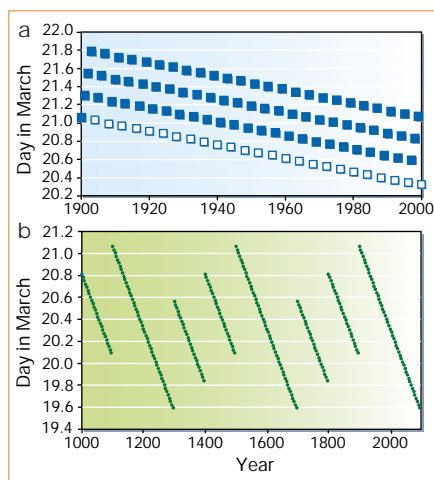


Figure 1 Trends in the calendar date of the vernal equinox (VE). Data are from a model produced by the Goddard Institute for Space Studies (<http://aom.giss.nasa.gov/svernal.html>). The model hindcasts and forecasts the times of equinoxes on the basis of a constant VE year of 365.2425 days. The actual VE year varies, and is currently closer to 365.2422 days; this discrepancy has a negligible effect on the bias reported here. **a**, Data for 1900–2000. The trend is driven by leap years (hollow symbols), which overcorrect for the yearly difference between the VE year and the 365-day calendar. **b**, Data for 1000–2099; one year out of every four is plotted. Because 2000 was a leap year, the trend towards earlier VE will continue until 2100.

towards earlier vernal equinoxes are broken at the beginning of most centuries and the equinox is ‘reset’ to a later date (Fig. 1b). This means that a given calendar date in spring will occur further from the vernal equinox towards the end of any century. As a result, trends towards earlier spring will tend to be overestimated.

The magnitude of this bias in reported phenological trends will depend on the length of the record, the period it covers, and the actual scatter of the data. As the magnitude of the bias cannot generally be predicted, I converted published data on examples of phenological events to express the time elapsed since the vernal equinox for each year of the data set, and compared linear trends between the original and transformed data sets.

My analysis of these examples showed biases of up to 10% in the originally reported trends (see supplementary information). Trends towards earlier spring are still significant, although generally smaller than the original data would indicate. Data sets that span the twentieth century show the largest bias. Although shorter-term data sets from the late twentieth century (see, for example, refs 1, 5, 7, 8) have smaller biases (1–5%), their biases will increase if they are extended into the twenty-first century for two reasons. First, the discrepancy between trends based on calendar dates and those based on proximity to the vernal equinox will continue to grow in the twenty-first century because the spring equinox will continue to become earlier until 2100 (Fig. 1b). Second, if the rate of global warming increases as expected and phenological trends follow accordingly, trends towards earlier spring in these data sets will be driven by the time period when the difference between calendar date and the date of vernal equinox is greatest.

Two data sets that span two previous centuries or longer² indicate that the advancement of spring may have been underestimated in some cases. This is probably an effect of unequal bias magnitude in data from successive centuries.

Although any underestimation of the delay of autumn events might be expected to offset bias in spring timing, most published phenological studies analyse spring events only. Reporting phenological events in relation to the vernal equinox is a simple procedure that does not require any change in data-collection methods. Phenological information is becoming more important for studying climate change because of the increased availability of long-term records¹¹, new methods for reconciling traditional records with recent remotely sensed data, and the incorporation of phenology into geographical-scale models¹². It is therefore essential that we

report phenological trends in terms that accurately reflect changes to the Earth system.

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Brood parasitism

Female ducks can double their reproduction

By engaging in extra-pair matings, the most successful males in some bird species can father twice as many young as are present in their own nest^{1,2}. Here we describe a female parallel in goldeneye ducks (*Bucephala clangula*), whereby some females can double their reproductive output by combining brood parasitism with normal nesting. This huge reproductive advantage should create strong selection for parasitic tactics.

We used protein fingerprinting by electrophoresis³ to trace the egg-laying patterns of individual females and determine the maternity of eggs in nests at Lake Mjörn in southwest Sweden^{3,4}. We marked incubating females individually with steel and colour rings, recorded the hatching success of clutches, marked chicks’ wings with numbered tags and brood-specific coloured tape, and recorded their survival over four weeks.

Numerical results are shown in Fig. 1a and represent the most intensive study year, 1986, in which the success of the different female tactics⁵ could be accurately estimated in a core study area from albumen samples taken from all 383 goldeneye eggs in 36 nests (7 of which were not incubated).

Three different female tactics seemed to be equally common: non-parasitic nesting, pure parasitism (laying only in the nests of other females), and parasitism followed by nesting (‘nesting parasites’) (Fig. 1). Observations of unmarked broods indicated that about 10% of nests were not discovered, and that edge effects may have led to underestimation of nesting parasites.

Acaenoplax — polychaete or mollusc?

Palaeozoic invertebrate fossils may pose severe problems in assigning them to Recent taxa. Sutton *et al.*¹ describe the beautifully preserved and illustrated Silurian fossil *Acaenoplax hayae* as a “plated aplacophoran” mollusc, interpreting its polychaete-like characters as convergent features. In our opinion, it is more parsimonious to place this organism in the Polychaeta, as the molluscan similarities are limited to serial valve-like structures, suggesting polyplacophoran affinities. It is unlikely that *Acaenoplax* represents a primitive organization that is neither molluscan nor polychaete — instead, it appears to represent a highly derived, specialized line of invertebrate evolution.

There is no evidence that the seven dorsal valves and one ventral valve of *Acaenoplax* were mineralized and hence molluscan. If they were originally aragonitic and similar to, for example, the polyplacophoran *Matthevia*, they would at best represent highly specialized structures within polyplacophorans^{2–4}; the plates of Silurian polyplacophorans⁵ are quite different. In addition, spicules in aculiferan molluscs are aragonitic rather than cuticular¹ and are scale-shaped in all basal molluscan classes. Spiny spicules are developed only in advanced Solenogastres and Polyplacophora and never emerge from transverse ridges or from plates.

Caudofoveata are adapted to a freely burrowing lifestyle, are covered by tiled scales, and have lost all traces of seriality (pseudo-metamery of dorsoventral musculature). This contrasts with the also infaunal but tube-dwelling habit of many sedentary polychaetes. The posteriorly shifted pallial cavity in Caudofoveata houses a single pair of gills; only in Solenogastres do multiple ‘protuberances’ exist in a ventro-medial (rather than terminal) pallial cavity. The terminal cavity of *Acaenoplax* is incompatible with the unrestricted, peripodal (surrounding the foot) pallial cavity of all known Polyplacophora. The combination of characteristics in *Acaenoplax*, when interpreted as a mollusc, results in a strange conglomerate that is not similar to Caudofoveata, to Polyplacophora, or to any primitive molluscan state¹.

The seriality common to Solenogastres and Polyplacophora refers only to their dorsoventral musculature, and affects neither the dorsal nor the lateroventral body region as in *Acaenoplax* (see Fig. 1j of ref. 1). Polyplacophora with reduced shell plates have mantle tissue that overgrows the plate margins; a ventral plate similar to that

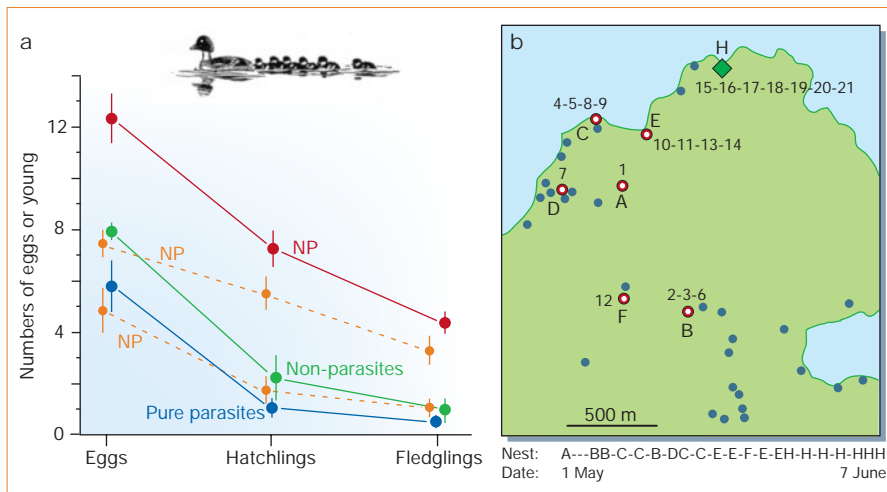


Figure 1 Reproductive tactics of female goldeneye ducks. **a**, Reproductive success (means \pm s.e.). Nesting parasites (NP; $n = 15$) first laid eggs in another female’s nest (parasitic, lower dashed orange line), and then in their own nest (parental, higher dashed orange line), producing in total (red line) many more eggs, hatchlings and fledglings per female than did pure parasites (blue; $n = 15$) and non-parasites (green; $n = 14$). Differences among the categories of female are statistically significant at each stage (eggs, hatchlings and fledglings; $P < 0.005$ after experiment-wise Dunn–Sidak correction). **b**, Distribution of parasitic laying sites (red, A–F) of the most successful nesting parasite in 1986, who laid 21 eggs in total. Numbers show the order in which she laid these eggs; grey dots represent other nest boxes. Date and nest site for each egg are shown at the bottom (dashes indicate days on which this female laid no eggs); the female laid her first parasitic egg (designated as 1 in nest A) on 1 May, the second (2) in another nest (B) on 5 May, and so on. After laying 14 parasitic eggs, the female laid and incubated 7 eggs (15–21) in her own nest (H, green square).

For 4 out of 15 nesting parasites, the shortest distance between a nest where the female had laid and the edge of the core study area was less than the median (for nesting parasites) of the maximum distance between a female’s own nest and a nest that she parasitized.

The three tactics differed strongly in reproductive success (Fig. 1a). Nesting parasites laid 12.3 eggs, 1.5 times as many as non-parasites (7.9), and twice as many as pure parasites (5.8). The most successful female laid 21 eggs (Fig. 1b), almost twice the previously supposed maximum for the species. In terms of chicks leaving the nest, nesting parasites out-reproduced non-parasitic females and pure parasites by more than 3:1 and 6:1 (7.3, 2.2 and 1.1 chicks, respectively). There is evidence that parasitic chicks survive just as well as the host’s own chicks⁶, in which case the advantage of nesting parasites is also present at the four-week stage (Fig. 1a).

How did nesting parasites achieve their high success? Their parasitic eggs resulted in fledgling numbers that are comparable to those from the host’s eggs. Also, nesting parasites later laid their own clutch, which was more successful than the earlier clutches of non-parasitic females as the risk of parasitism-related disturbance and nest desertion or predation decreased over the season. Eggs hatched out in 13 of 15 nesting-parasite nests, but in only 5 of 14 non-parasite nests ($P = 0.0078$).

There is no evidence that reduced survival or reproduction in later years nullifies the reproductive advantage of nesting parasitism, and there were no obviously

special circumstances in 1986 that would have promoted the success of nesting parasites. Their proportions were comparable in other years (our unpublished results).

These results point to a fitness advantage for nesting parasites: by combining parasitism with normal nesting, some female goldeneye ducks more than doubled their reproduction. This raises questions as to why females differ in their reproductive tactics and about the long-term fitness costs and benefits of the different tactics. There is evidence that tactics are flexible — we found that many females switched tactics between years (our unpublished results; see also refs 6–10). Nesting parasites may also be in their prime (with high egg-laying capacity). Nesting parasites had been breeding for fewer previous years (1.9 ± 0.29) than non-parasitic females (2.7 ± 0.60), but the difference is not statistically significant ($P = 0.24$). The implications of the different reproductive strategies need further investigation.

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