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# Conflict between biotic and climatic selective pressures acting on an extended phenotype in a subarctic, but not temperate, environment

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Climatic selective pressures are thought to dominate biotic selective pressures at higher latitudes. However, few studies have experimentally tested how these selective pressures differentially act on traits across latitudes because traits can rarely be manipulated independently of the organism in nature. We overcame this challenge by using an extended phenotype—active bird nests—and conducted reciprocal transplant experiments between a subarctic and temperate site, separated by 14° of latitude. At the subarctic site, biotic selective pressures (nest predation) favoured smaller, non-local temperate nests, whereas climatic selective pressures (temperature) favoured larger local nests, particularly at colder temperatures. By contrast, at the temperate site, climatic and biotic selective pressures acted similarly on temperate and subarctic nests. Our results illustrate a functional trade-off in the subarctic between nest morphologies favoured by biotic versus climatic selective pressures, with climate favouring local nest morphologies. At our temperate site, however, allocative trade-offs in the time and effort devoted to nest construction favour smaller, local nests. Our findings illustrate a conflict between biotic and climatic selective pressures at the northern extremes of a species geographical range, and suggest that trade-offs between trait function and trait elaboration act differentially across latitude to create broad geographic variation in traits.

## 1. Introduction

Traits that vary geographically are commonly thought to represent adaptations to spatially variable selective pressures [1]. These spatially variable selective pressures show consistent patterns with elevation and latitude, with climatic factors thought to dominate biotic interactions in colder environments [2–5]. Reviews support a greater role for climatic selective pressures relative to biotic selective pressures at higher elevations and latitudes [5–8] (but see [9,10]), but experimental tests of how selection acts on geographically variable traits in nature are uncommon, particularly across latitudes [5,6].

Testing how climatic and biotic factors act on geographically variable traits is challenging because specific traits are difficult to isolate from other covarying traits within individuals [11]. This obstacle could be overcome if a trait could be transplanted into different selective regimes independent of the individual that produced that trait. Behaviours that result in a physical structure external to the organism (i.e. an extended phenotype [12]), such as a bird nest, present cases where geographical variants of a trait can be physically moved between environments, independent of the organism's other traits. These extended phenotypes thus provide a unique opportunity to examine how climatic and biotic selective pressures act on specific local and non-local traits within and across environments, independent of the individual that constructed them.

We conducted reciprocal transplant experiments on active yellow warbler (*Setophaga petechia*) nests between a subarctic and a temperate breeding site to examine how climatic and biotic selective pressures act on geographically
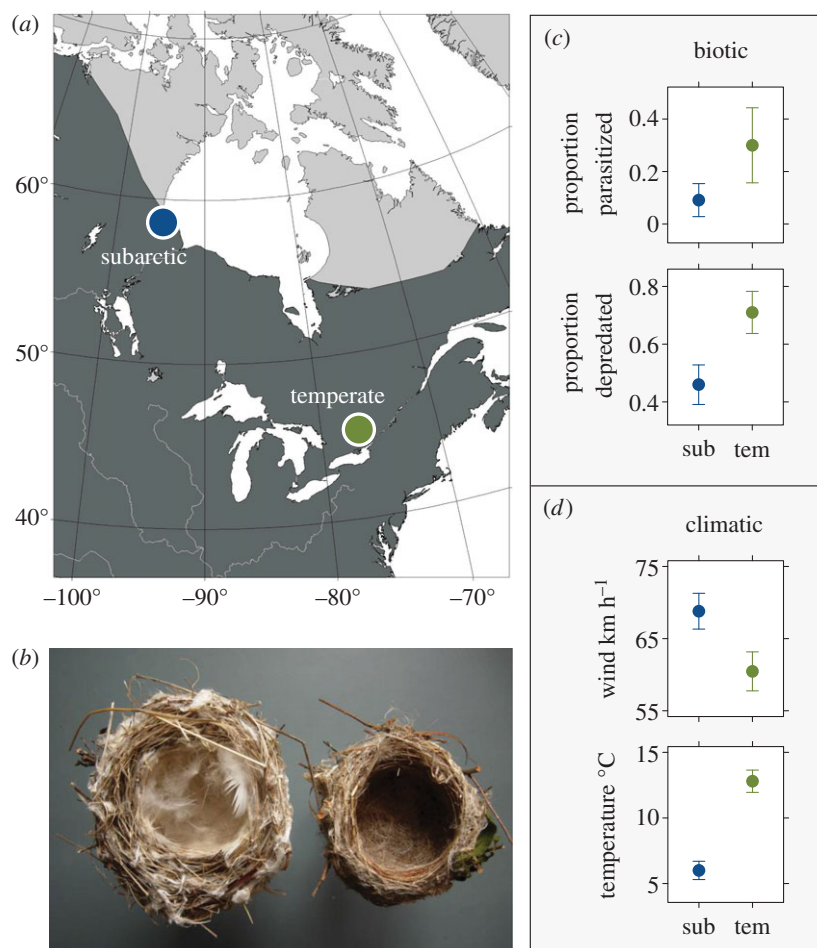
**Figure 1.** Differences between subarctic and temperate breeding sites. (a) Subarctic and temperate sites are separated by approximately 2000 km, and 14° latitude; dark grey area on the map indicates yellow warbler breeding distribution. (b) Typical nests from the subarctic (left) and temperate (right) sites; subarctic nests are larger and better insulated than temperate nests [23]. (c,d) Differences (mean $\pm$ 1 s.e.) in (c) biotic and (d) climatic challenges confronting breeding yellow warblers between subarctic (sub) and temperate (tem) sites: the proportion of nests parasitized by arthropod ectoparasites, proportion of nests that failed because of nest predation (c), and wind speeds (maximum gusts), and average minimum temperature during the breeding season (d). Proportion data are from control nests at each location and standard errors were estimated from 1000 bootstrapped simulations; climate data are from [24]. Climatic factors were more challenging at the subarctic site compared to the temperate site, while biotic factors were relatively more challenging at the temperate site ($p < 0.05$, all comparisons). (Online version in colour.)

variable nest morphologies at different latitudes. Nest morphologies are an ideal trait in which to examine differential selection by climatic and biotic selective pressures because they are under strong selection from both factors [13,14]. Birds must maintain nest temperatures near 36–40°C for optimal embryo and nestling development [13], and thus cold ambient temperatures present a climatic challenge that should favour large, well-insulated nests. By contrast, nest predation is the most common cause of nest failure in many bird species [15], including yellow warblers [16], and presents a strong selective pressure for nest morphologies that reduce the likelihood of predation. Selection from nest predators may favour small nests that are less conspicuous [17] and cryptic nests constructed with materials that reduce contrast with the local background environment [18]. The importance of nests for successful reproduction in birds, coupled with strong biotic and climatic selection on nest morphologies, suggest that geographic variation in nest morphologies will be related to the relative importance of climatic versus biotic selective pressures acting between sites. Although geographic variation in nest morphologies is observed across a diversity of birds and nest-building rodents, the selective mechanisms favouring this variation is poorly understood [19–21].

Subarctic and temperate sites differ in the magnitude and nature of climatic versus biotic selective pressures, and these differences are thought to underlie the dramatically different nest morphologies of yellow warblers breeding at these two sites [22,23] (figure 1). The subarctic site is located near Churchill, Manitoba, Canada, at the northern limit of the breeding distribution of yellow warblers, whereas the temperate site is located in southeastern Ontario, Canada, closer to the centre of the breeding range of this species. At both sites, yellow warblers typically place their nests in short deciduous shrubs low to the ground (less than 2 m) [16]. During the breeding season, the subarctic site is colder, drier and windier than the temperate site [19], and these climatic conditions challenge yellow warblers to maintain warm nest temperatures and to regulate water loss from eggs and young [25]. By contrast, biotic selective pressures of nest predation and ectoparasitism are significantly higher at the temperate site (figure 1).

To experimentally test how climatic and biotic selective pressures act on local versus non-local nest morphologies, we conducted a total of 198 transplants (subarctic $n = 115$, temperate $n = 83$) during the 2008–2012 breeding seasons. During early incubation, we replaced nests constructed by local females with either local nests constructed by different females

or non-local nests from the opposite location (see video in electronic supplementary material). Females never altered the morphology of transplanted nests at either location, allowing us to examine how selection operated on different nest morphologies within sites. For nest transplants at both sites, we measured nest success, number of unhatched eggs, causes of nest failure, nest microclimate and nest ectoparasite infestation. Upon finding differences between treatment groups in these measures at the subarctic site, but not at the temperate site, we also measured adult incubation behaviour, adult female and nestling corticosterone (stress hormone) levels and nestling growth rates for subarctic nest transplants. We predicted that local nest morphologies would have higher nest success. For the subarctic site, we predicted that adult incubation behaviours would reflect differences in selective pressures, with less activity and longer incubation bouts associated with higher predation risk [26], and shorter bouts off the nest associated with an increased challenge of cold temperatures [27]. We predicted nestling growth rates (an indicator of nestling quality and future survival [28]) would be fastest in local nests, and that corticosterone levels of both adult females and nestlings would be elevated or atypical in non-local nests compared with local nests [29,30].

## 2. Results

Nest transplants at the subarctic site revealed conflicting selection between biotic and climatic factors. Surprisingly, non-local temperate nests fledged one young per nest more, on average, than local subarctic nests (hurdle model, $p = 0.014$; figure 2). This difference in the number of young fledged was caused by lower predation on non-local temperate nests (Cox regression, $p = 0.0035$; figure 2). Levels of nest ectoparasitism did not differ between local and non-local nests (see the electronic supplementary material).

While nest predation at the subarctic site favoured small, non-local nests, cold ambient temperatures favoured thicker local nests. Non-local temperate nests had colder average and minimum temperatures compared with local subarctic nests (GLM and LME, respectively, $p < 0.021$; figure 3a); laboratory experiments confirm that the larger, better-insulated subarctic nests retain more heat than poorly insulated temperate nests [23]. Nestlings in non-local temperate nests also grew more slowly than nestlings in local subarctic nests (GLM, $p = 0.004$), and this effect was strongest at cold temperatures (GLM treatment × temperature interaction, $p = 0.029$; figure 3b). We found no significant difference between local and non-local nests in incubation duration, female incubation behaviours, male mate-feeding during incubation, the number of unhatched eggs, the number of nests that failed due to cold temperatures, or adult female and nestling corticosterone levels (see the electronic supplementary material).

In contrast to the subarctic site, nest transplant experiments at the temperate site revealed no differences in selection by biotic and climatic factors, and no evidence for selection in favour of local or non-local nests. Local and non-local nests had similar nest predation rates (figure 2b), similar levels of ectoparasite infestation (electronic supplementary material) and fledged similar numbers of young per nest (figure 2b). Local and non-local nests also showed no differences in nest temperatures and humidities (figure 3a; electronic supplementary material), and no difference in the number of unhatched
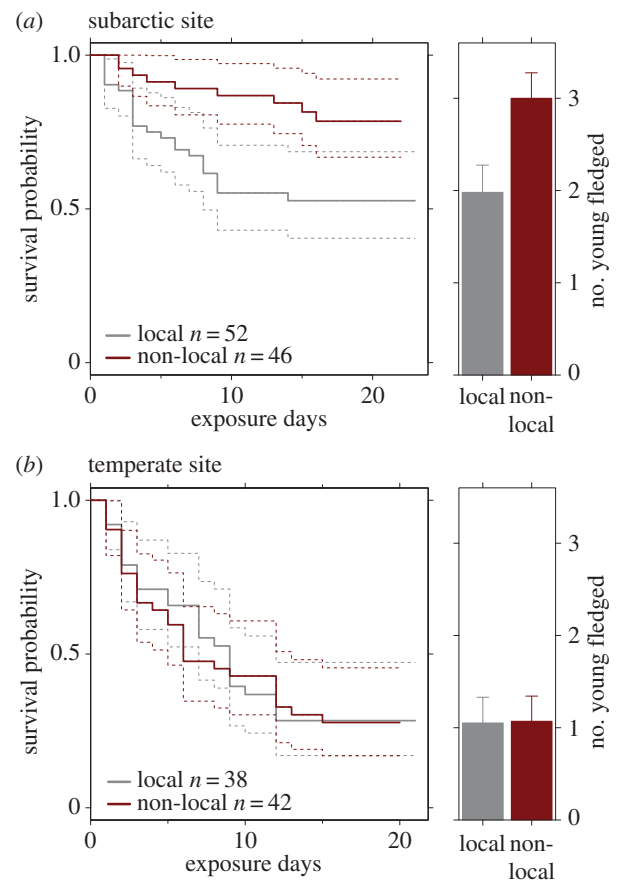


**Figure 2.** Biotic costs for transplanted local and non-local nests at the subarctic and temperate sites. Costs of nest predation illustrated by Kaplan–Meier survival curves ($\pm$ 95% CI) and average ($\pm$ 1 s.e.) number of young fledged per nest for transplanted local and non-local nests at the (a) subarctic and (b) temperate site. At the subarctic site, local nests suffered higher predation ($p = 0.0035$) and fledged on average one nestling fewer compared to non-local nests ($p = 0.014$). At the temperate site, local and non-local nests suffered similar levels of predation (log rank test: $\chi^2 = 0.0$, $p = 0.88$) and fledged similar numbers of young ($p = 0.99$). (Online version in colour.)

eggs (electronic supplementary material). Overall, transplanting subarctic nests to our temperate site revealed no evidence for biotic or climatic selection against subarctic nest morphologies in a temperate environment.

While transplant experiments at the temperate site suggest no cost to using non-local subarctic nests, larger subarctic nests required more time and effort to build. We filmed the entire nest-building process for five nests at each site and found that females constructing temperate nests made, on average, 467 trips to and from the nest, while females constructing subarctic nests made 1248 trips (two-tailed $t$-test, $p < 0.004$). Temperate females also spent less time at the nest site during construction (two-tailed $t$-test, $p = 0.015$) and tended to allocate fewer days to nest building, compared with subarctic females (figure 4).

Temperate nests were not smaller because of a limited availability of nesting materials. In the early stages of nest construction, we presented eight temperate-breeding females with nest material from one temperate and one subarctic nest so that females had access to ample material to create a subarctic-sized nest. All eight females used materials that we presented to them (see the electronic supplementary material). The eight supplemented nests, however, were indistinguishable from temperate nests for all three measures
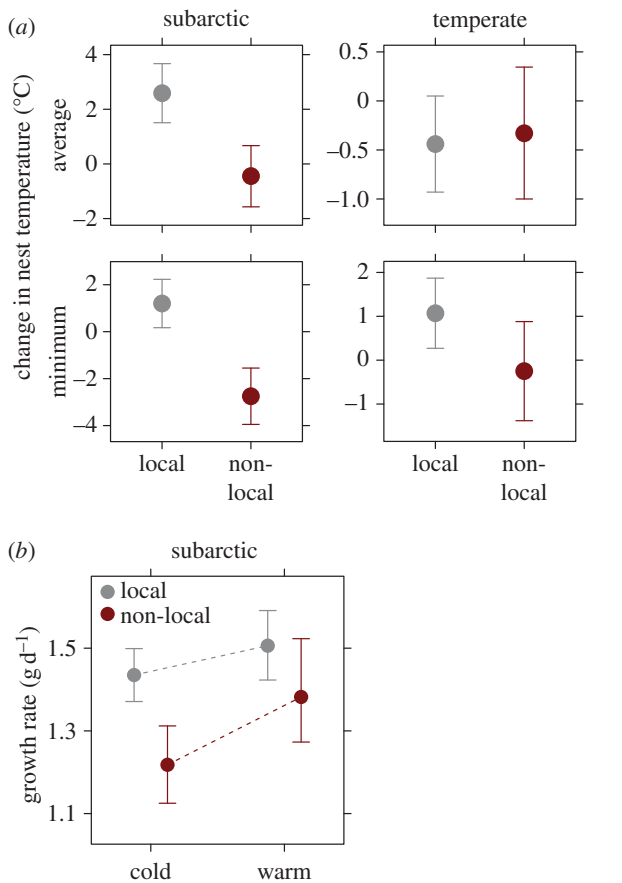
**Figure 3.** Climatic costs for transplanted local and non-local nests at the subarctic and temperate sites. (*a*) Changes in average and minimum nest temperatures after nest transplants (post-transplant − pre-transplant temperature values), between local and non-local nests at subarctic (left) and temperate (right) sites; points are means ± 1 s.e. At the subarctic site, non-local temperate nests had colder average ($p = 0.01$) and colder minimum ($p < 0.002$) temperatures compared to local subarctic nests, while at the temperate site, local and non-local nests had similar average ($p = 0.90$) and minimum ($p = 0.37$) temperatures. Local and non-local nests did not differ in maximum nest temperature or measures of humidity at subarctic and temperate sites (electronic supplementary material). (*b*) Average growth rates (± 95% CI) of nestlings in transplanted local and non-local nests at the subarctic site. Nestlings in non-local nests grew more slowly ($p < 0.008$, local $n = 21$, non-local $n = 29$), especially during cold temperatures ($p = 0.029$), compared with nestlings in local nests; categories 'cold' and 'warm' correspond to minimum ambient temperatures of 5.4 − 9.1°C and 9.2 − 13.1°C, respectively, recorded during the period that we measured nestling growth rate. (Online version in colour.)

of external morphology (exterior nest depth, nest-wall thickness, exterior cup diameter; Mann–Whitney *U*-test, $p > 0.25$), but were significantly smaller in these measures compared with subarctic nests (Mann–Whitney *U*-test, $p < 0.05$). See table 1 for a summary of results, and the electronic supplementary material for detailed methods and statistical summaries of the analyses presented above.

# 3. Discussion

Transplanting an extended phenotype—bird nests—from a temperate to a subarctic site revealed conflict between biotic and climatic selective pressures acting on nest morphologies in a subarctic environment. Local subarctic nests provided greater insulation and a warmer microclimate favourable for
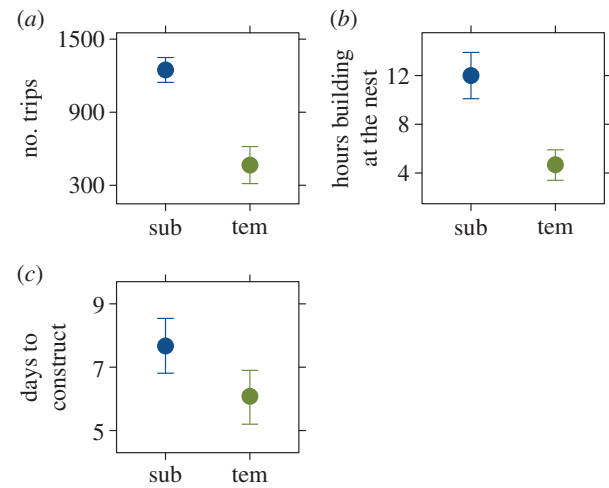


**Figure 4.** Time and effort to construct subarctic and temperate nests. Plots show (*a*) the average (± 1 s.e.) number of trips a female made to construct her nest, (*b*) the average (± 1 s.e.) amount of time a female spent at her nest during construction and (*c*) the average (± 1 s.e.) number of days required to construct the nest for $n = 5$ females at both the subarctic (sub) and temperate (tem) sites. Females constructing subarctic nests made more trips ($p < 0.004$) and spent more time at the nest site during construction ($p = 0.015$), but took similar numbers of days to construct their nests ($p = 0.23$), compared with females constructing temperate nests. (Online version in colour.)

**Table 1.** Summary of results from analyses testing whether local or non-local nest morphologies were favoured for transplanted nests at subarctic and temperate sites. Italic type indicates statistically significant differences between local and non-local nest morphologies within a site.

| | subarctic | temperate |
|---|---|---|
| trait or selective pressure | favoured nest morphology | favoured nest morphology |
| nest predation rate | *non-local* | no difference |
| nest ectoparasites | no difference | no difference |
| nest temperature | *local* | no difference |
| nest humidity | no difference | no difference |
| number of young fledged | *non-local* | no difference |
| number of unhatched eggs | no difference | no difference |
| incubation duration | no difference | not measured |
| parental behaviour | no difference | not measured |
| nestling growth rates | *local* | not measured |
| adult female corticosterone levels | no difference | not measured |
| nestling corticosterone levels | no difference | not measured |

developing eggs and young (figure 3*a*). Similarly, nestlings in local subarctic nests grew at a faster rate compared with nestlings in non-local temperate nests, particularly at colder temperatures (figure 3*b*). Given that nestling growth rate is a positive predictor of future survival in passerine birds [28], investing in thick local nests may provide important long-term advantages for young warblers after leaving the nest. In contrast, biotic selective pressures, in the form of nest

predation, favoured non-local, temperate nests, with temperate nests fledging one young per nest more, on average, than local subarctic nests (figure 2a). The lower predation rates on non-local temperate nests may have been caused by their smaller relative size, their cryptic coloration or their novel phenotype lying outside of the search image of subarctic predators. These results illustrate a conflict between climatic and biotic selective pressures in the subarctic, with local nest morphologies reflecting a phenotype most favoured by climate.

In contrast to the subarctic, nest transplants at the temperate site revealed similar patterns of selection acting on nest morphologies. Non-local subarctic and local temperate nests had similar microclimates and rates of nest predation and parasitism, and fledged similar numbers of young (figures 2 and 3). The differences in nest predation rates between nest types at the subarctic site, but not at the temperate site (figure 2), may be caused by environmental differences between the sites, such as the timing of nest construction prior to leaf development in the subarctic that might allow easier visual detection of phenotypic differences between nests, or by differences in the predator communities, where major temperate nest predators (snakes [31]) locate nests using adult movement or olfactory cues rather than the visual cues of nests [32,33]. The results suggest that climatic and biotic selective pressures act similarly on the different nest morphologies in the temperate environment and that subarctic or temperate nests are equally suitable for reproduction.

Instead of selection acting on nest morphologies, selection at the temperate site may act on the time and effort allocated to nest construction, thus favouring smaller, local nests. Large, subarctic nests required significantly more time and trips to construct (figure 4), and these added costs of nest construction provided no measurable benefit at our temperate site (figures 2 and 3). Higher rates of nest predation in temperate environments should further favour reduced investment in nest construction because females renest following nest depredation. Indeed, some females constructed as many as five nests within a single breeding season (V.G.R., personal observation), augmenting the costs of nest construction across the season and pressuring females to construct nests quickly to ensure a successful reproductive attempt before the end of the breeding season.

Trade-offs between selective pressures, such as those evident at our subarctic site, may constrain the distributions of species at the limits of their geographical ranges [6,34,35]. For yellow warblers, the subarctic site occurs at the extreme northern limit of their range. With lower temperatures at higher latitudes, warblers face an increasing challenge of optimizing nest phenotype to maintain temperatures between 36 and 40°C to maximize embryo and nestling development (a highly conserved thermal requirement across birds [13]), while minimizing the costs of nest predation and nest construction. Conflict among selective pressures may be strongest at range limits where organisms are often pushed to physiological, metabolic or competitive limits [36–39], or lack associate species important for survival and reproduction [40,41]. This balancing between conflicting selective pressures that vary geographically may prove important for determining the viability of populations at the limits of their ranges, as has been suggested in plants [42], aquatic invertebrates [43] and fishes [44].

Overall, our results suggest that biotic and climatic selective pressures acting on an extended phenotype in yellow warblers

conflict at a subarctic site, but not at a temperate site, creating a functional trade-off in optimal nest morphology in the subarctic. Our experiments illustrate that subarctic yellow warblers create a phenotype favoured by climate and disfavoured by biotic pressures (nest predation), consistent with predictions by Darwin [2], Wallace [3] and others [4,5] that climatic selective pressures influence traits more strongly at higher latitudes. In contrast to the functional trade-offs evident at our subarctic site, the additional time and effort required to build large subarctic nests suggest an allocative trade-off that should constrain the size of nests across all environments. Such trade-offs should generally constrain the development of more costly phenotypes—phenotypes that are increasingly favoured as environmental temperatures diverge from optimal temperatures for organismal performance [45].

# 4. Material and methods

## (a) Nest transplants

To conduct a transplant, we either waited for females to naturally leave their nests, or we flushed females by approaching the nests. Once at the nest, we carefully removed eggs and placed them temporarily into a cotton-filled container, then removed the female's nest and replaced it with either a local nest from the same site (but constructed by a different female) or a non-local nest from the opposite study site. We then carefully returned the female's eggs into the transplanted nest (see video in electronic supplementary material). Whether a female received a local or non-local nest was decided randomly using a coin toss for the first nest that we found in each location; we then alternated between local and non-local nests for all subsequent transplants.

## (b) Changes in nest temperature and humidity

We measured temperature and humidity from inside active nests before and after transplants by burying iButton data loggers (Hydrochron DS 1923; Maxim Integrated Products Inc., CA, USA) beneath 1–2 mm of the nest lining, directly under the eggs. We calculated changes in nest temperature and humidity by subtracting pre-transplant values from post-transplant values, which allowed us to control for variation in nest microclimate between nest sites, and for differences in incubation behaviours of individual females. All measures of temperature and humidity come from paired comparisons of local and non-local nests measured simultaneously (spanning the exact same dates and times) to control for temporal variation in weather.

## (c) Parental behaviour during incubation

We measured changes in five parental behaviours: (i) frequency of off-bouts (number of off-bouts $h^{-1}$, where off-bouts are time intervals when the female is away from the nest), (ii) average off-bout duration, (iii) average on-bout duration (where on-bouts are time intervals when the female is on the nest, incubating eggs), (iv) the proportion of time spent on the nest and (v) the frequency of male feeding visits to incubating females on the nest (male visits $h^{-1}$). We measured parental behaviours both before and after nest transplants—allowing us to control for variation in nest microclimate and parental behaviour of individual parents—by filming nests in the early morning (starting between 4.00 and 4.30) for 4–6 h. We then calculated the change in parental behaviours as (values after the transplants) − (values before the transplants). All changes in parental behaviours come from paired comparisons of transplanted local and non-local nests filmed simultaneously to control for possible changes in behaviour due to weather.

## (d) Adult female corticosterone

We captured females during late incubation (between incubation days 7 and 9) by flushing them directly from their nest into mist nets. We measured baseline corticosterone (cort) levels from circulating blood by taking small blood samples (approx. 100 µl) from the brachial vein; all blood samples used in our analyses were collected in under 3 min from when the female first hit the mist net [46]. We measured total levels of cort from blood plasma using direct radio-immunoassays, following extraction with redistilled dichloromethane (see [47] for details).

## (e) Incubation duration

We tested for differences in incubation duration between local and non-local transplant nests at the subarctic site only. We defined the start of incubation as the date of clutch completion and the end of incubation as the date when at least half the eggs had hatched, and predicted non-local nests would have longer incubation durations compared with local nests.

## (f) Nestling growth rates

We weighed nestlings from local and non-local nests on days 2 and 6, and recorded time of day to control for the number of hours between weighing events (recorded in days to the nearest 0.1 days). We calculated nestling growth rates as weight gain in grams per day via [(average nestling mass on day 6) − (average nestling mass on day 2)]/(time interval between weighing in days). We calculated average nestling mass by dividing the total brood mass by the number of nestlings at the time of weighing.

## (g) Nestling corticosterone

We measured cort levels from $8 \pm 1$-day-old nestlings in local and non-local nests at the subarctic site only. We collected small blood samples (approx. 100 µl) from at least one nestling (per nest) in under 3 min from when we first approached the nest [46]; processing blood and measuring cort followed the same procedures for adult females above.

## (h) Nesting success and survival analyses

We first tested if the number of young fledged within a site differed between local and non-local nests, using hurdle models for transplants at the subarctic site, and generalized linear models with a Poisson distribution corrected for overdispersion (quasi-Poisson) at the temperate site. We included all transplanted nests (abandoned, depredated and successful) within a site to examine the overall effects of treatment on the number of young produced at each site.

To examine if climatic and biotic selective pressures acted differently on local and non-local transplant nests within each site, we estimated mortality rates that were primarily caused by climate and predation independently, following previously published methods [48–50].

We tested if predation and climate differentially influenced the success of local and non-local transplant nests at each site using Cox proportional hazards regressions in the *survival* package [51] in R [52]. We performed two Cox regressions for transplants at the subarctic site—one for nest failure caused by predation and one for nest failure caused by climate. We performed only a single Cox regression for nest failure caused by predation at the

temperate site; we did not perform a Cox regression for climate-caused failure at the temperate site because only two nests at this site were believed to have failed due to climate (one local nest and one non-local nest). See the electronic supplementary material for detailed methods of survival analyses.

## (i) Nest ectoparasites

We tested if local and non-local transplant nests differed in the number or diversity of nest ectoparasites at each site by collecting transplanted nests that successfully fledged young or that survived until nestlings reached at least 5 days of age. We carefully dissected nests and counted the number of parasites in each nest.

## (j) Nest construction

To assess the time and effort required to construct subarctic and temperate nests, we filmed the entire nest-building process for five nests at each site and scored three components of nest-building behaviour: (i) the total number of trips females made to the nest site during building, (ii) the total number of hours spent actively building the nests (e.g. weaving or manipulating material at the nest itself) and (iii) the total number of days spent building the nest. Subarctic nests are larger than temperate nests [23], thus we predicted they would require more time and trips to construct.

## (k) Material supplementation

We examined if the availability of nesting material limited nest size at the temperate site by providing eight temperate-breeding females (that were in the early stages of nest construction) with supplemental nest material from one complete temperate and one complete subarctic nest. We then compared nest morphology (nest-wall thickness, exterior nest diameter and exterior nest depth) of the eight supplemented nests with unsupplemented temperate and unsupplemented subarctic nests.

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