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Author(s) :L. M. Evans, R. W. Hofstetter, M. P. Ayres, and K. D. Klepzig

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Temperature Alters the Relative Abundance and Population Growth Rates of Species Within the *Dendroctonus frontalis* (Coleoptera: Curculionidae) Community

L. M. EVANS,[1,2,3] R. W. HOFSTETTER,[4] M. P. AYRES,[1] AND K. D. KLEPZIG[5]

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ABSTRACT Temperature has strong effects on metabolic processes of individuals and demographics of populations, but effects on ecological communities are not well known. Many economically and ecologically important pest species have obligate associations with other organisms; therefore, effects of temperature on these species might be mediated by strong interactions. The southern pine beetle (*Dendroctonus frontalis* Zimmermann) harbors a rich community of phoretic mites and fungi that are linked by many strong direct and indirect interactions, providing multiple pathways for temperature to affect the system. We tested the effects of temperature on this community by manipulating communities within naturally infested sections of pine trees. Direct effects of temperature on component species were conspicuous and sometimes predictable based on single-species physiology, but there were also strong indirect effects of temperature via alteration of species interactions that could not have been predicted based on autecological temperature responses. Climatic variation, including directional warming, will likely influence ecological systems through direct physiological effects as well as indirect effects through species interactions.

KEY WORDS species interactions, indirect interactions, climate change, community structure, physiological ecology

Climate is a major determinant of arthropod distributions and demography (Ayres 1993, Bale et al. 2002, Parmesan 2006). Understanding how climate change will affect arthropod populations remains a priority (Dale et al. 2001, Easterling et al. 2007). Both interactions among species and autecological factors, such as climatic variables, strongly affect populations (Ayres 1993, Wootton 1994, Bale et al. 2002, Nahrung et al. 2004). Although evidence exists that species will respond individualistically to climate change (Bale et al. 2002, Parmesan 2006) such individual responses can disrupt interactions, leading to changes in communities (Petchey et al. 1999, Walther et al. 2002, Voight et al. 2003). Because of such disruptions, species' responses within communities might be qualitatively different from individual responses (Davis et al. 1998, Petchey et al. 1999, Walther et al. 2002, Voight et al. 2003, Barton et al. 2009, Hoekman 2010); therefore, a major goal of global change research is to understand effects within a community context.

Understanding how pest species will respond to climate change is a critical challenge (Dale et al. 2001, Crozier et al. 2006, Easterling et al. 2007, Seppälä et al. 2009). The frequency and severity of insect pest outbreaks are expected to be influenced by climate change, resulting from the strong effects of abiotic factors (e.g., temperature and plant water stress) on insect development (Easterling et al. 2007, Seppälä et al. 2009). However, many pest species have direct and indirect interactions with numerous other species, providing multiple pathways for climate change to affect the system (Ayres and Lombardero 2000). For example, bark beetles in the genus *Dendroctonus* harbor phoretic mites and fungi that affect beetle population dynamics (Goldhammer et al. 1990, Paine et al. 1997, Six and Paine 1998, Hofstetter et al. 2006a, Adams and Six 2007, Cardoza et al. 2008). Because demographic effects of temperature differ among these species (Lombardero et al. 2003, Hofstetter et al. 2006a, Six and Bentz 2007), how climate change will affect beetle dynamics might not be easily predicted. Other examples of pest species with intimate associates include *Amylostereum* fungi and woodwasps (Slippers et al. 2003), pinewood nematodes and cerambycid beetles (Linit 1988), and bacterial endosymbionts of numerous insects including termites, aphids, and whiteflies (Moran and Telang 1998). Responses to temperature may differ among these interacting species, making it necessary to consider effects on inter-

[1] Department of Biological Sciences, Dartmouth College, Hanover, NH 03755.
[2] Corresponding author, e-mail: lme36@nau.edu.
[3] Current address: Biology Department, Northern Arizona University, Flagstaff, AZ 86011.
[4] School of Forestry, Northern Arizona University, Flagstaff, AZ 86011.
[5] Southern Research Station, USDA Forest Service, Asheville, NC 28804.

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actions when studying the effects of climate change. Here, we studied the effects of temperature on an economically important insect pest, *Dendroctonus frontalis* Zimmermann, and its associated mites and fungi within communities.

The southern pine beetle, *Dendroctonus frontalis* Zimmerman, is native to North America and attacks and kills native pines from New Jersey to Honduras. It occasionally reaches epidemic abundances, making it among the most important forest pests in North America (Thatcher et al. 1980). Population fluctuations in *D. frontalis* are partly the result of delayed negative feedback from coupled interactions with a specialist predator (Turchin et al. 1991), but the tendency for endogenous cycles is weaker than previously thought (Friedenberg et al. 2007), and there is accumulating evidence for strong demographic effects from interactions involving symbionts of *D. frontalis* (Klepzig et al. 2001, Hofstetter et al. 2006a).

Dendroctonus frontalis has a strong mutualism with two species of mycangial fungi, *Entomocorticium* sp. A and *Ceratocystiopsis ranaculosus* Hausner. The fungi receive selective transport (within mycangia) to new host trees and the beetle larvae feed on fungal-enriched phloem within trees (Barras and Perry 1972). The fungi only occur in association with the beetles and almost all female adult beetles (>90%) carry one or the other of these fungi (Hofstetter et al. 2006a). *Entomocorticium* tends to be a better nutritional source than *C. ranaculosus* (Coppedge et al. 1995), and beetle populations grow faster when a higher proportion of females carry *Entomocorticium* (Bridges 1983). *Dendroctonus frontalis* also transport many species of phoretic mites among host trees (Moser 1975). *Tarsonemus* mites, which are particularly common, are mutualists with a bluestain fungus (*Ophiostoma minus* Hedgecock), which they selectively transport to new host trees, propagate within trees and then consume (Bridges and Moser 1983, Lombardero et al. 2000). *Ophiostoma minus* might initially aid beetles in overcoming tree resistance (Klepzig et al. 2005), but overall is a strong antagonist of *D. frontalis* larvae, apparently because it outcompetes the mycangial fungi and is itself of poor nutritional value for beetles (Barras 1970, Klepzig and Wilkins 1997). Natural populations of *D. frontalis* tend to grow when *O. minus* is rare and decline when *O. minus* is abundant (Hofstetter et al. 2006a). Because *Tarsonemus* mites promote *O. minus*, they are strong indirect antagonists of *D. frontalis* (Lombardero et al. 2003, Hofstetter et al. 2006a).

Because of the number and complexity of strong interactions, there are multiple pathways through which temperature could affect the southern pine beetle system. For example, autecological studies show that the growth rate of *Tarsonemus* populations is more sensitive to temperature than the development time of *D. frontalis*, implying that the antagonistic effects of mites on beetles would be greatest at ≈27°C and drop off rather sharply as temperatures increase or decrease from there (Lombardero et al. 2003). Furthermore, the two mycangial fungi differ in their temperature responses (Klepzig et al. 2001). Based on their autoecological responses, cooler temperatures should favor *Entomocorticium* relative to *C. ranaculosus* (Hofstetter et al. 2007), which should be beneficial to *D. frontalis*. Alternatively, the most important effects of temperature might arise from more complex mechanisms: e.g., interactions between *Tarsonemus* and other species of mites that alter interactions among fungi that influence beetles. To evaluate these possibilities we manipulated the temperature experienced by communities within trees naturally colonized by *D. frontalis* and their associates.

Materials and Methods

Experimental Design. We conducted two similar experiments. In both cases, we identified a set of similar adjacent trees (6–7, ≈25 cm diameter at breast height (dbh) and 18 m tall) that were being simultaneously attacked by the same population of *D. frontalis*, sampled the parental attacking beetles to characterize the incoming community of phoretic mites and fungi, waited until all attacks had ceased (indicating the period of oviposition and egg hatch within the phloem), then felled the trees, cut 6–8 replicate 40-cm bolts from the mid-bole of six or seven trees, and transported those to environmental chambers where they were distributed across temperature treatments. We collected, counted, and measured the emerging adult progeny, and examined them for phoretic symbionts. Our first study (experiment 1) began in July 2004 with seven slash pine (*Pinus elliottii* Engleman) in the Chickasawhay Ranger District, DeSoto National Forest, MS. The second study (experiment 2) began in October 2004 with six loblolly pine (*Pinus taeda L.*) in the Oakmulgee Ranger District, Talladega National Forest, AL. Both *Pinus* species are suitable hosts for *D. frontalis*, though *P. taeda* is generally regarded as more susceptible and perhaps more suitable (Thatcher et al. 1980). In both studies, we placed four Lindgren funnel traps (unbaited) among the study trees to collect 150–200 live free-flying attacking beetles (collected over 2–4 d during the peak of attacks on study trees) that we stored individually at 1°C and later examined for phoretic mites and fungi Hofstetter et al. 2006a). We identified mites to genus (chiefly *Tarsonemus*, *Dendrolaelaps*, *Trichouropoda*, and *Histiogaster*; identity confirmed by Dr. John Moser, USDA Forest Service Southern Research Station, Pineville, LA), and also scored each beetle for presence of *O. minus* (experiment 1 only) and each female beetle for presence of the two mycangial fungi, *C. ranaculosus* and *Entomocorticium* sp. A (both experiments), following the methods of Hofstetter et al. (2006). We dissected and mounted the mycangium of each female in lactophenol blue dye to identify *C. ranaculosus* and *Entomocorticium* sp. A under a compound microscope (Barras and Perry 1972, Bridges 1983, Hofstetter et al. 2006a). To determine presence of *O. minus* on the beetles, we plated each individual on 10% malt agar to grow cultures of the fungus.

We randomly assigned two bolts per tree (one each from the lower and upper region of the mid-bole) into

each of four or three (experiments 1 and 2, respectively) temperature regimes. The target temperatures were 23, 25, 27, and 32°C for experiment 1 and 23, 28, and 33°C for experiment 2. Mean daily temperatures in our study region range from 7 to 28°C over the year, and daily maxima regularly exceed 30°C during summer (www.noaa.gov). Thus, our experiment spanned temperatures from cool to warm relative to typical summer conditions in the Gulf Coastal region of the United States. Our treatments were also designed to range above and below 27°C, which was the predicted optimum for reproduction by *Tarsonemus* mites based on autecological measurements (Lombardero et al. 2003). We conducted experiment 1 at the USDA Forest Service Research Station in Pineville, LA, and experiment 2 at Dartmouth College in Hanover, NH. Facilities permitted one more temperature treatment in Louisiana but somewhat better temperature regulation at Dartmouth. We recorded the actual temperatures every 5 min throughout the experiment with one or more HOBO (Onset Computer Corporation, Pocasset, MA) temperature loggers per treatment: mean temperatures ± SD were: 22.8 ± 2.4, 25.5 ± 2.7, 26.0 ± 1.9, and 31.5 ± 2.6°C for experiment 1, and 23.6 ± 0.8, 28.4 ± 0.9, and 33.4 ± 1.6°C for experiment 2.

Beetle, Mite, and Fungal Measurements. We placed each bolt in a container with a collection cup for emerging beetles. We collected emerging beetles daily and kept them at −5°C. After beetle emergence, we measured the length and circumference of each bolt and estimated the number of attack holes We estimated the number of attacks per log by sequentially slicing thin layers of the outer bark and marking entrance holes (each representing the attack of one male-female pair). *Dendroctonus frontalis* entrance holes are usually within bark fissures, tend to enter somewhat obliquely, and generally show evidence of resin flow (hardened resin or crystals), whereas exit holes tend to be perpendicular to the bole of the tree and are frequently within rather than between bark plates. For each bolt, we removed two 20.5 by 16 cm sections of bark and measured percentage of phloem with bluestain (indicating *O. minus*) and length of oviposition gallery by tracing onto mylar acetate (Hofstetter et al. 2006a). We digitized the tracings and measured them using the program Raster to Vector© (www.raster-vector.com). To determine mite abundance within the phloem, we also counted *Tarsonemus* and non-*Tarsonemus* mites on three randomly placed one-cm^2 squares in areas within bluestain and three in areas with no bluestain (Lombardero et al. 2003). We multiplied the average abundance per 1-cm^2 by the total area within each bolt for bluestained and non-bluestained phloem separately, and then summed to give the total number of *Tarsonemus* per bolt at the end of the experiment.

We collected over 4,000 emerged beetles in each experiment. The first emergences were parent beetles that reemerged after mating and oviposition. Subsequent emergences were the progeny, which had developed from egg to adult during the experiment. We separated the reemerging beetles from progeny based upon a clear trough in the number of emerging beetles (Fig. 1). We calculated the development time (day of emergence), per capita reproductive success (λ = progeny per attacking adult), and the mean day of progeny emergence for each bolt. We compared development time to the time predicted by the biophysical model of Wagner et al. (1984).

To allow for possible patterns with respect to timing of beetle development, we subsampled beetle progeny from three stages of beetle emergence (early, peak, and late). We defined peak emergence for each bolt as the date of maximum emergence per day ± 1 d, and early and late as dates (±1 d) when cumulative emergence was 40% less or more (respectively) of that on the date of maximum emergence. We examined this subset of beetles for phoretic mites and fungi as before and also measured female beetle length because length is positively correlated with fecundity (Coppedge et al. 1995).

We estimated *Tarsonemus* reproductive success within each bolt, R, calculated from mite abundance within the phloem at the end of experiment. We estimated the initial population size as the mites per beetle in the parent generation multiplied by the number of adult beetles that entered the bolt (twice the number of attack holes), and R was calculated as: $|\ln(N_{final} + 1) - \ln(N_{initial})|/d$. The addition of one was required to avoid excluding a few bolts from which no mites were recorded in the phloem. For comparison, we also calculated the expected mite R for each temperature treatment. Lombardero et al. (2003) estimated mite population growth rate (mites per mite per day) at different temperatures in the laboratory. Using the recorded temperature in each of our treatments at 5-min time steps and these growth rate estimates (calibrated to 5-min time steps), we calculated the expected mite growth rate (R) in each temperature treatment. Because variation will introduce bias in nonlinear relationships (Jensen's Inequality; Ruel and Ayres 1999), using 5-min time steps allowed us to accurately account for imperfect temperature regulation, and is why our predictions of mite growth rates do not exactly match those of Lombardero et al. (2003).

Statistical Analyses. For most response variables, we tested for temperature effects with an analysis of variance (ANOVA) model that included temperature, tree, and temperature x tree as fixed effects. Because of unequal sample sizes for each bolt, we averaged response variables within each bolt. No beetles emerged from two trees at the highest temperature, so we excluded these trees from the analyses. We log transformed λ and arcsine-square root-transformed proportion of bluestained in phloem. We analyzed mites per beetle for each mite genus using an ANOVA with full factorial design including temperature, stage, and tree as fixed effects, as well as the interaction terms. To analyze the effect of temperature treatment on the proportion of beetles with each fungus, we used χ^2 tests (Sokal and Rohlf 1995). We performed the statistical tests by using JMP V. 5 (SAS Institute 2002).

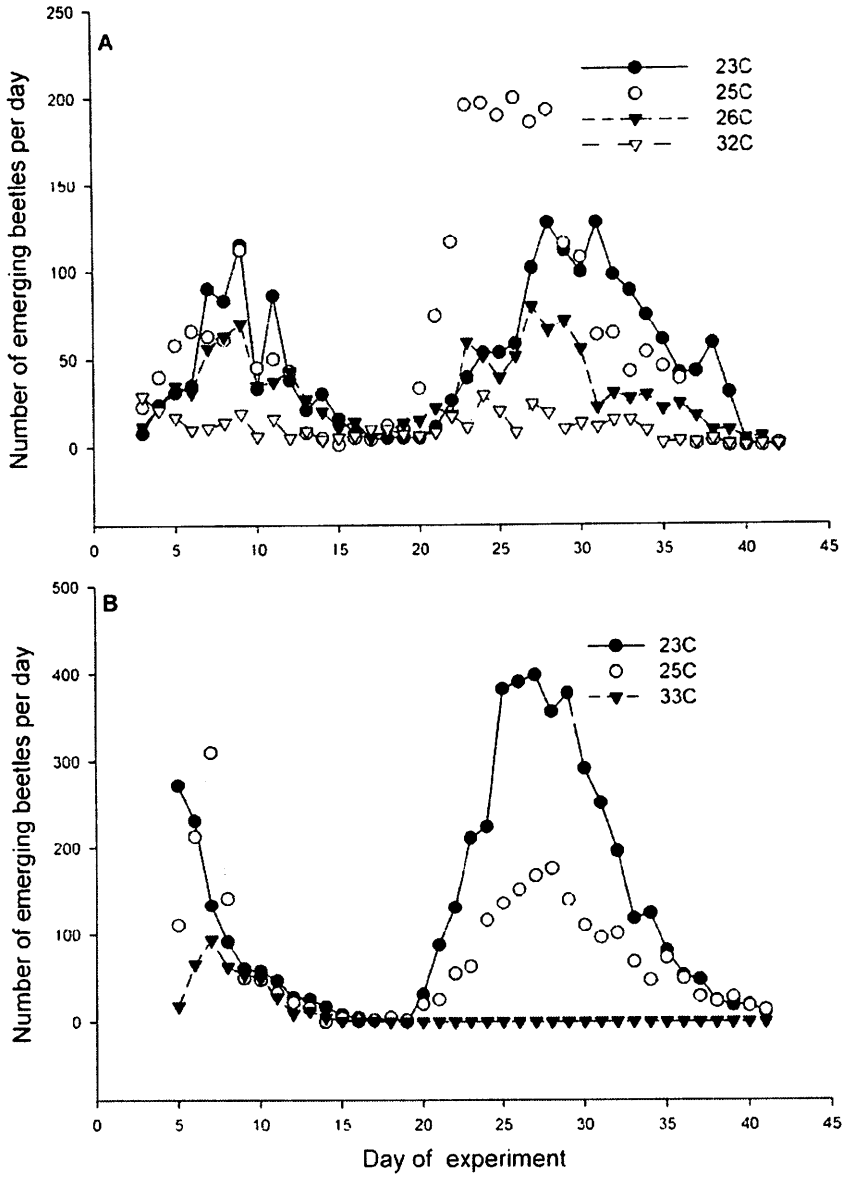

Fig. 1. The number of *D. frontalis* emerged each day varied among temperatures in experiment 1 (A) and experiment 2 (B). The first peak represents reemerging adults from the parental generation, while the second peak represents emerging adult progeny beetles.

Results

Initial Conditions. Attack densities did not differ among temperature treatments: grand mean ± 1SE = 2.91 ± 0.13 and 3.33 ± 0.08 attacks per dm^2 in experiments 1 and 2 (Table 1). The length of oviposition gallery did not vary with temperature in experiment 1 (91.45 ± 0.10 cm/dm^2) and varied among temperatures in experiment 2 (59.77 ± 2.55, 60.80 ± 2.55, and 43.68 ± 2.55 cm/dm^2 at 23, 28, and 33°C) (Table 1).

In both experiments, the parental female beetles were about equally split between those carrying *Entomocorticium* versus *C. ranaculosus* in their mycangia, but there were more females that carried neither in experiment 1 (number of individuals in each category 21:25:12 and 11:8:1 in experiments 1 and 2, respectively; Fig. 3). The percentage of attacking beetles carrying the bluestain fungus, *O. minus*, was 15.5 and 40.1% for each experiment. Phoretic mites were also common: the mean (±SEM) initial abundances of *Tarsonemus*, *Dendrolaelaps*, *Trichouropoda*, and *Histiogaster* per beetle were 1.79 (0.26), 1.04 (0.18), 1.87 (0.34), and 0.43 (0.07) in experiment 1 and 3.56 (0.88), 0.27 (0.15), 0.40 (0.14), and 0.00 (0.00) in experiment 2, respectively.

Beetle and Mite Reproduction and Transmission of Fungi. Beetle reproduction was higher in experiment 2 than in experiment 1, but declined markedly with increasing temperature, from λ of $\approx$ 0.8–0.2 in exper-

Table 1. ANOVA F-ratios of *D. frontalis* bolt attack density, no. of re-emerging parental beetles, gallery density, reproduction, and proportion of bluestained phloem

Source	df	No. Re-emerging								Proportion *O. minus* Phloem	
		Attack Density		Adults		Gallery Length		Beetle λ			
		Slash	Lob.	Slash	Lob.	Slash	Lob.	Slash	Lob.	Slash	Lob.
Temp.	3, 2	1.01	2.14	8.90**	7.10**	0.65	14.20***	4.93**	47.90***	13.31***	10.71***
Tree	6, 5	2.26	0.59	7.70**	0.11	0.52	6.37**	1.20	1.21	6.01**	3.79*
Temp. × Tree	18, 10	0.45	1.24	1.30	2.13	0.93	7.80***	0.54	1.19	0.75	1.66

Degrees of freedom, df, refer to slash and loblolly experiments, respectively.
Asterisks signify statistical significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.
Error degrees of freedom are 28 for slash pine and 35 for loblolly pine.

iment 1 and 2 .1–0 in experiment 2 (Fig. 2A). Temperature effects were conspicuous compared with variance among individual trees, which was undetectable (Table 1). Temperature did not affect size of adult progeny in experiment 1 (mean ± SEM = 2.81 ± 0.02 mm) and only slightly in experiment 2 (2.89 ± 0.02 versus 2.68 ± 0.02 mm at 23 versus 28°C; Table 2). Beetle development time generally matched predictions of the model of Wagner et al. (1984), with the greatest departure being that beetles in the 23°C treatment in experiment 2 emerged 4 d earlier on average than predicted (Fig. 2B; Table 2).

Temperature manipulations altered the relative abundance of mycangial fungi in adult progeny beetles (experiment 1: $\chi^2 = 23.12$, df = 6, $P = 0.00076$; experiment 2: $\chi^2 = 5.35$, df = 2, $P = 0.069$; Fig. 3). In both experiments, the percentage of beetles with *Entomocorticium* in their mycangium declined with increasing temperature. In experiment 2, this was compensated by an increase in *C. ranaculosus*, whereas in experiment 1 the proportion of beetles without mycangial fungi increased (to 36% at 32°C).

In both experiments, the abundance of the bluestain fungus, *O. minus*, decreased from ≈20 to 5% of the phloem colonized with increasing temperature (Fig. 2C; Table 1). The proportion of emerging progeny beetles with *O. minus* inoculum on the exoskeleton also decreased at higher temperatures, but this trend was not significant (experiment 1: 26.8, 22.2, 21.9, 10.5% with inoculum at 23, 25, 27 and 32°C, respectively; $\chi^2 = 4.20$, df = 3, $P = 0.24$). Beetle reproduction decreased with increasing proportion of bluestained phloem only at the lowest temperature in experiment 2 ($F = 10.87$; df = 1, 10; $P = 0.008$); however, in all other treatments there was no relationship ($P > 0.05$; Fig. 4).

The per capita reproduction of *Tarsonemus* mites decreased with increasing temperature (Fig. 5; Table 3). The pattern was a poor match to the autecological prediction that reproduction should have been greatest at intermediate temperatures. Realized per capita growth rate was negative in all treatments except 25°C in experiment 1.

Temperature affected phoretic mite abundance, but the patterns varied among genera of mites (Fig. 6; Table 4). The abundance of phoretic *Tarsonemus* declined as temperatures increased in experiment 1 but not experiment 2. In contrast, the abundance of

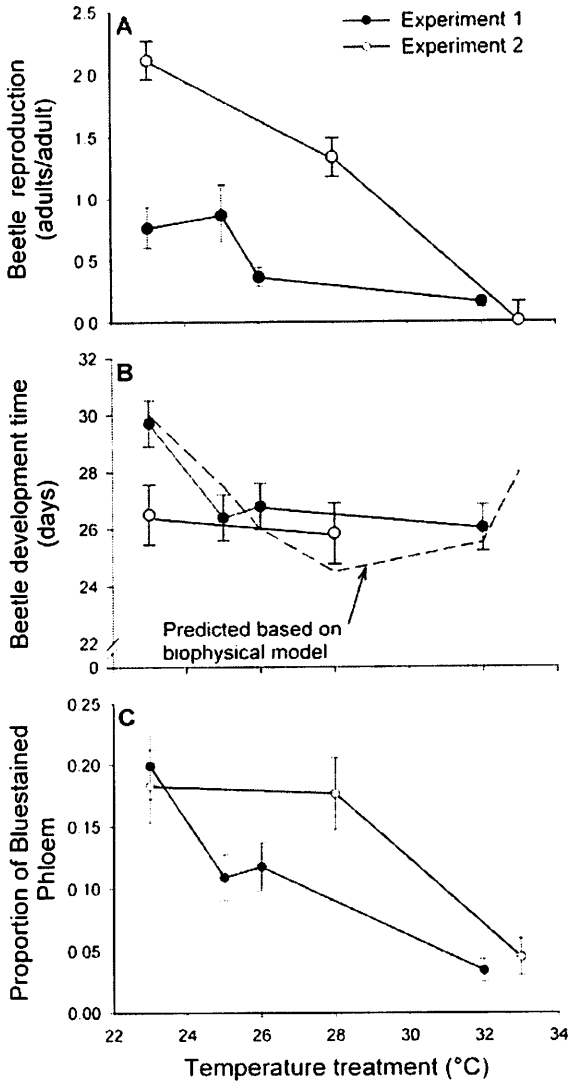

Fig. 2. (A) *D. frontalis* reproduction observed at each temperature treatment. No beetles emerged at the highest temperature in experiment 2. (B) Observed *D. frontalis* development time at each temperature treatment. Dashed line represents the predicted development time from a biophysical model (Wagner et al. 1984). (C) The proportion of phloem colonized by *O. minus*. In all panels means ± SEM are shown.

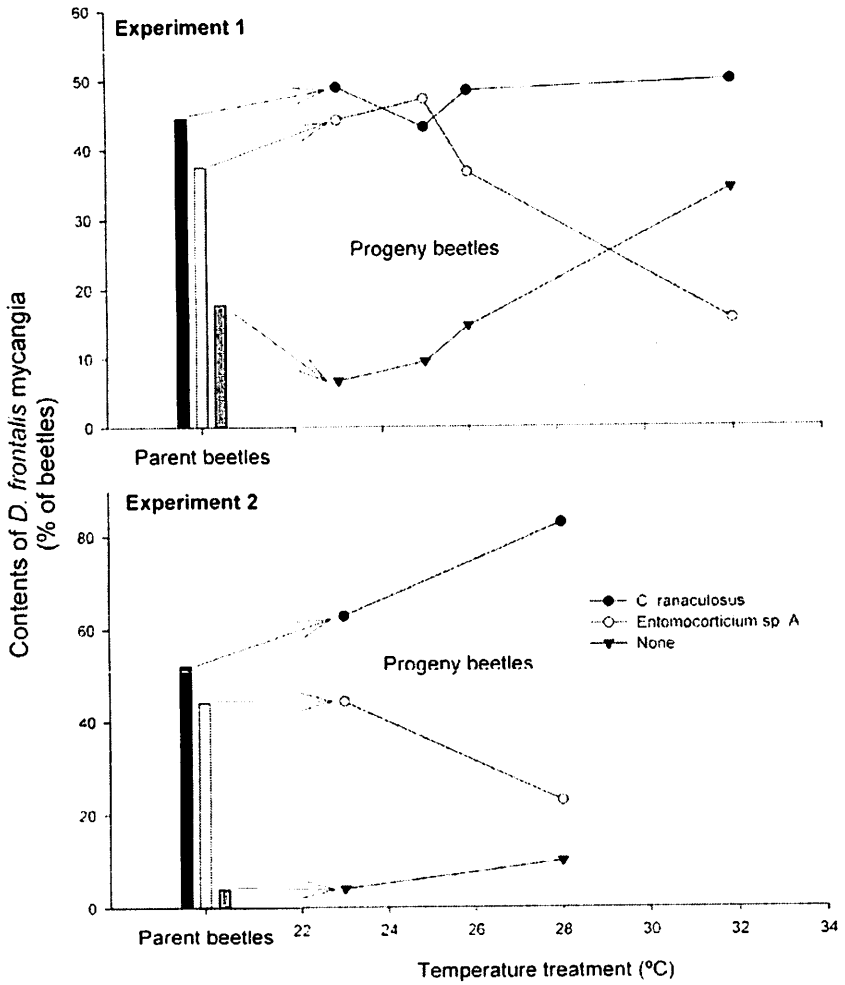

Fig. 3. Relationships between beetle reproduction (λ) and phloem bluestain abundance within experiment 1 (A) and experiment 2 (B) for each temperature treatment.

Trichouropoda, *Histiogaster*, and to a lesser extent, *Dendrolaelaps*, tended to increase from 23 to 26°C. With further temperature increases, the abundance of *Dendrolaelaps* and *Trichouropoda* remained stable, while that of *Histiogaster* dropped sharply, and were not found in experiment 2.

Table 2. ANOVA F-ratios of *D. frontalis* size and development time (mean day of emergence)

Source	Beetle length (mm)			Mean day of Emergence		
	df	Slash	Lob.	df	Slash	Lob.
Temp.	3, 1	0.64	8.70*	3, 1	1.32*	0.20
Tree	4, 5	1.37	1.14	6, 5	1.09	0.55
Temp. × Tree	12, 5	0.31	1.32			
Error	12, 11			18, 11		

Degrees of freedom, df, refer to slash and loblolly experiments, respectively.

Asterisks signify statistical significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.0001$.

Discussion

Experimental manipulation of temperature altered the relative abundance and relative population growth rates of species within the *D. frontalis* community. *Dendroctonus frontalis* population dynamics are influenced by both climate (Ungerer and Ayres 1999, Gan 2004) and interactions with other species (Barras 1973; Bridges 1983; Goldhammer et al. 1990; Turchin et al. 1991; Lombardero et al. 2003; Hofstetter et al. 2006a, 2007). Results indicated direct effects of temperature on species' development and survival, and suggested further indirect effects from changes in species interactions, supporting the view that communities are structured by both autecological responses of species to environmental factors as well as effects on strong interactions among species.

Direct effects of Temperature on Beetles. *Dendroctonus frontalis* reproduction decreased at higher temperatures in both experiments, possibly from direct physiological consequences. Even though attack densities were similar among treatments fewer parental

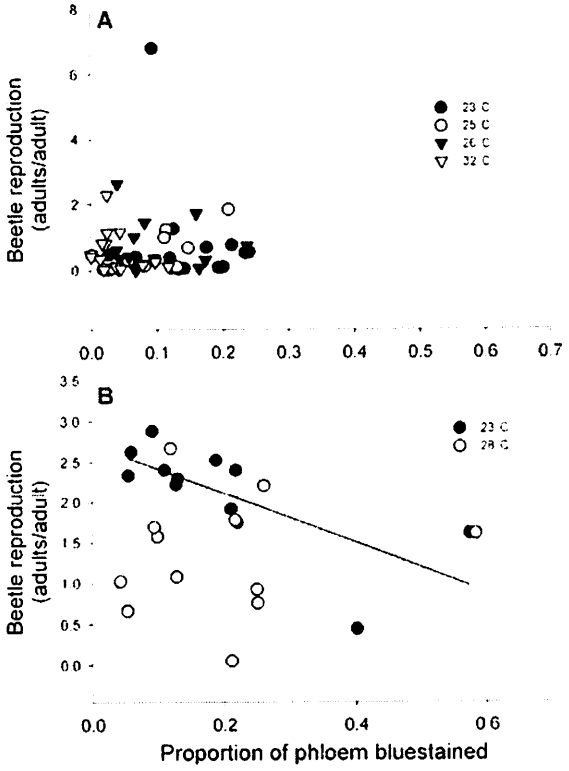

Fig. 4. Percent of beetles with each mycangial fungus, or none.

beetles reemerged at higher temperatures, indicating increased mortality (Fig. 1; Table 1). As reemerged females might oviposit in other host trees (Thatcher et al. 1980), higher temperatures might directly reduce lifetime beetle reproduction because of increased mortality.

Temperature affected beetle reproduction through direct effects on progeny. Gallery length (a surrogate for egg number, Lashomb and Nebeker 1979) was similar among treatments (Table 1); thus, differences in the number of progeny reflected differences in

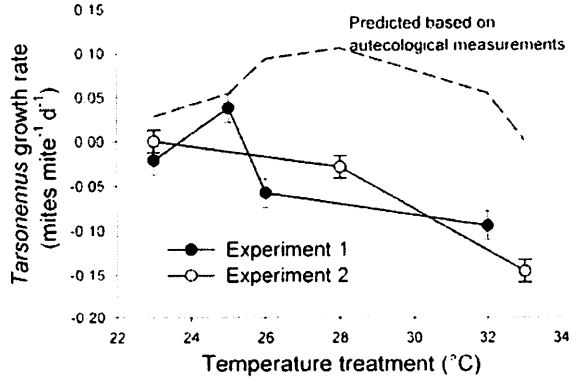

Fig. 5. Growth rate (R; mean ± SEM) of *Tarsonemus* mites within the phloem of experimental bolts. Predicted R (dashed line) is based on autecological measurements of mites in *O. minus* cultures (Lombardero et al. 2003).

Table 3. ANOVA F-ratios of *Tarsonemus* growth rates (R) based on reproduction within the phloem

Source	df	R Slash	R Lob.
Temp.	3, 2	12.10***	34.44***
Tree	6, 5	2.52	1.27
Temp. × Tree	18, 10	1.34	1.17
Error	28, 17		

Degrees of freedom, df, refer to slash and loblolly experiments, respectively.

Asterisks signify statistical significance: *** $P < 0.0001$.

survival during development. Temperature had little effect on progeny size, but median development time decreased with increasing temperature in experiment 1. Treatment effects on development time were less evident in experiment 2 (probably partly because logs spent 4 d en route to New Hampshire and therefore spent somewhat less time in temperature treatments), but in both experiments, development time approximated the projected development time based on a biophysical model of *D. frontalis* development (Fig. 2B; Wagner et al. 1984). Temperatures were relatively constant during both experiments, compared with natural diurnal fluctuations in field conditions. Even the highest temperature treatment encompasses temperatures regularly experienced by beetles in the field, but high field temperatures have been reported to reduce beetle population growth and brood survival (Thatcher and Pickard 1964, Gagne et al. 1980, Friedenberg et al. 2008). Our results support this and other earlier work (Wagner et al. 1984), despite differences in diurnal temperature fluctuations. Host species might have also driven differences observed between the two experiments, because pines differ in suitability for *Dendroctonus* (Langor et al. 1990, Veysey et al. 2003). The tendency for better beetle reproduction in experiment 2 (Fig. 2A) might have occurred because *P. taeda* is a better host than *P. elliottii* (Hodges et al. 1979, Thatcher et al. 1980). Collectively, these results indicate strong direct effects of temperature on *D. frontalis* reproductive success.

Effects of Temperature on Species Interactions. In addition to the direct effects of temperature, interactions with *O. minus*, *Tarsonemus*, or mycangial fungi might have affected beetle reproduction. High abundance of *O. minus* (bluestain) generally yields poor survival of beetle larvae (Barras 1970, Lombardero et al. 2003, Hofstetter et al. 2006a). We found a significant relationship between bluestain and beetle λ in only one treatment, probably because the abundance of bluestain in phloem was generally below the threshold of ≈40% where effects tend to be strongest (Figs. 2C and 4; Hofstetter et al. 2006a). Differences among pine species affect the performance of Ophiostomatoid fungi (Cook and Hain 1988, Hofstetter et al. 2005, Rice et al. 2007); therefore, the slightly higher proportion of bluestained phloem in the second experiment might have resulted from higher host quality of *P. taeda* for *O. minus*. However, overall there was little bluestained phloem, and little evidence that temperature effects

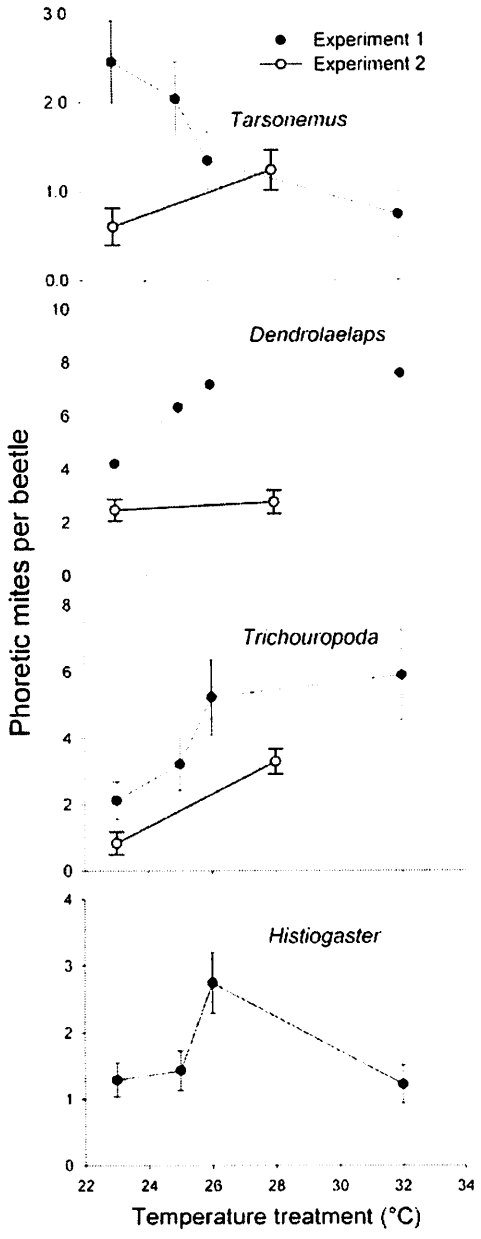

Fig. 6. Phoretic mites per progeny beetle (means ± SEM) in. No *Histiogaster* mites occurred in the second experiment, and no beetles emerged at the highest temperature of experiment 2.

on *D. frontalis* reproduction were related to changes in the abundance of its fungal antagonist, *O. minus*.

Tarsonemus abundance strongly influences beetle reproduction (via introduction and propagation of *O. minus*); therefore, temperature effects on *Tarsonemus* tend to affect *D. frontalis* in the next generation (Lombardero et al. 2003). Both of our experiments indicated that *Tarsonemus* per emerging progeny was elevated at low to intermediate temperatures (Fig. 6) implying negative demographic effects of those temperatures on *D. frontalis* via temperature effects on *Tarsonemus*. However, the effect of temperature on *Tarsonemus* populations did not match the predicted autecological measurements (Fig. 5; Lombardero et al. 2003) indicating that temperature effects on *Tarsonemus* within a community are more complicated than expected from direct physiological effects. Tarsonemus mite abundance was not directly related to *O. minus* abundance in phloem (Figs. 2C, five and 6), contrary to other studies with higher bluestain abundances (Lombardero et al. 2003, Hofstetter et al. 2006a).

Temperature effects on interactions among species might explain patterns in *Tarsonemus* reproduction. *Histiogaster* and *Trichouropoda*, (fungivores and scavengers) and *Dendrolaelaps* (predators) all have the potential to interact with *Tarsonemus* through resources competition or predation (Moser and Roton 1971, Moser 1975). In experiment 1, *Tarsonemus* reproduction decreased sharply from 25 to 26°C (Figs. 5 and 6), which coincided with sharp increases in *Histiogaster*, *Dendrolaelaps*, and *Trichouropoda* abundances (Fig. 6). In experiment 2, where *Histiogaster* was rare or absent, *Tarsonemus*, *Dendrolaelaps*, and *Trichouropoda* abundances were positively correlated across temperatures (Fig. 6). We speculate that *Histiogaster* might be a strong antagonist of *Tarsonemus*, presumably via resource competition, and that temperature mediates their interactions.

Experiments indicated further indirect effects of temperature related to mycangial fungi (nutritional symbionts) abundance on *D. frontalis*. Both fungi showed clear responses to temperature, but results differed slightly between the two experiments (Fig. 3). This might be because of host differences in secondary metabolites that could alter the relative performance of the fungi (Hofstetter et al. 2005, Rice et al. 2007), though we are aware of no studies that have examined differences between *P. taeda* and *P. elliottii* on fungal performance. Regardless of the potential tree effects, *Entomocorticium sp. A* performed poorly at high temperatures. The decrease in *D. frontalis* λ at high temperatures could be a direct result of poor mycangial fungal growth (Goldhammer et al. 1990, Coppedge et al. 1995). Furthermore, future reproduction at the highest temperatures would be limited as a high proportion of emerging beetles had no mycangial fungi, which leads to decreased reproductive success. Constant temperatures in the treatments depart from field conditions, and periodic, rather than constant, high temperatures might buffer their effects. However, our experimental results match expectations from observations in the field for fungi associated with both *D. frontalis* (Hofstetter et al. 2006b) as well as *D. ponderosae* (Adams and Six 2007, Six and Bentz 2007); thus, experimental results are likely relevant to field dynamics. While temperature might have had direct effects on *D. frontalis*, indirect effects via mutualistic fungi had clear consequences for beetle reproduction, which could then affect associated species (e.g., phoretic mites).

Temperature had an opposite effect on *C. ranaculosus*, the other nutritional symbiont of *D. frontalis*. *Ceratocystiopsis ranaculosus* was either not affected by

Ubcrh 5/ BOPWB Gsbujpt pgqi psfujd n juf bcvoebodft gpvoe po f n f shjoh E/ gspoubrjt qsphf oz/ Op l jtujphbtuf sx f sf gpvoe po cf f urht f n f shjoh gspn rpcrpmma qjof /

Tpvsdf	eg	Ubstpofn vt		Efoesprbfrbqt		Usjdi pvspqpeb		I jtujphbtuf s
		Trbti	Mpc/	Trbti	Mpc/	Trbti	Mpc/	Trbti
Usf f	5-6	4/19+	5/21++	28/87++	5/51++	9/39++	2/82	42/: 3+++
Uf n q/	4-2	4/9: +	5/33+	2/73	1/34	4/15	34/2: +++	4/69+
Uf n q/ × Usf f	23-6	3/73+	4/42+	5/21	3/94+	3/4: +	2/83	6/54++
Tubhf	3-3	22/15++	2/35	1/86	3/24	1/42	1/16	34/32+++
Usf f × Tubhf	9-21	1/85	1/53	1/82	1/33	2/72	1/56	7/28++
Uf n q/ × Tubhf	7-3	5/. 5++	2/53	1/7:	1/6:	1/93	1/32	1/58
Uf n q/ × Usf f × Tubhf	35-21	3/67+	1/45	2/18	1/6:	1/94	1/57	2/8:

Efhsf f t pggsf f epn - eg- sf gf s up trbti boe rpcrpmma f yqf sjn f ou- sf tqf djwf ra/
Btuf sjt l t tjhojgz tubujtjdbmtjhoj· dbodf ; + Q.< 1/16- ++ Q.< 1/12- +++ Q.< 1/1112/
Fssps ef hsf f t pggsf f epn bsf 2: gps trbti qjof boe 44 gps rpcrpmma qjof /

uf n qf sbuvsf) f yqf sjn f ou2* ps jujodsf btf e jo bcvo. ebodf x ju jodsf btjoh uf n qf sbuvsf) f yqf sjn f ou 3< Gjh/ 4*/ Jujt bqppsf sovusjujpobmtpvsdf) Csjehf t 2: 94* boe dpn qf ujups) Lrfhq{jh boe X jrhjot 2: : 8* ui bo Fo. upn pdpsujdjvn tq/ B- cvujut cf of · uef qf oet po uf n . qf sbuvsf / Jut hsf buf s tvddf tt bui jhi f s uf n qf sbuvsf t dpvrma brtp sf tpnvf ui f rvf tujpo pg x i z ui jt gvohvt qf stjtut x ju jo ui f tztuf n - boe brtp i px ju{jowbef eÿ ui f E/ gspoubrjt tzn cjptjt) Tjy boe Lrfhq{jh 3115*/ Gspn ui f tf sf tvrnt- pof dpvrma qsf ejduui buopsui f so ps i jhi f rfwbujpo dpn n vojujf t bttpdjbuf e x ju E/ gspoubrjt ti pvrma ti px jodsf btf e bcvoebodf t pg Foupn pdpsuj. djvn tq/ B- cvuui buqbuf sot n jhi uejggf s bn poh i ptu usf f tqf djf t/ B tjn jrbs qbuf so i bt cf f o gpvoe jo ui f E/ qpoef sptbf tztuf n - x i f sf uf n qf sbuvsf ef uf sn joft ui f sf rbujwf bcvoebodf pgux p tzn cjpujdgvohj) Tjy boe Cf ou{ 3118* <ui f sf gpsf - ejggf sf oujbmui f sn bmuprfhsbodf t pgn zdbohjbmgvohj n jhi ucf bdpn n po gf buvsf pgcbsl cf f urh n vwbrjtn t/

Dpodmatjpot/ Uf n qf sbuvsf bnf sf e ui f sf rbujwf bcvoebodf t boe hspx ui sbuf t pg E/ gspoubrjt boe jut bttpdjbuf e n juf t boe gvohj/ Ui f tf uf n qf sbuvsf f gf dut x f sf opubma bzt tjn jrbs up ui ptf gspn tuvejf t pgjoej. wjevbmtqf djf t- cvujotuf be sf tvrnf e gspn ui f jo, vf odf pg uf n qf sbuvsf po tuspoh jouf sbdujpot x ju jo ui f E/ gspoubrjt dpn n vojuz/ Bt bo f svqujwf f dpopn jdbma boe f dprphjdbma jn qpsubou qf tu tqf djf t- voef stuboejoh x i bugbdupst jo, vf odf ui f qpqvrbujpo ezobn jdt pgE/ gspoubrjt jt dsjujdbmqbsjdvrbsma jo ui f gbdf pg drjm buf di bohf) Fbtuf srjoh f u brh 3118- Tf qqbMf u brh 311: */ X i jrh ejsf duf gf dut pg drjm buf di bohf po Ef oespdup. ovt bsf cf joh pctf swf e) Dbsspmfi ubrh 3115*- ui jt tuvez boe pui f st) I pgtuf uf sf ubrh 3118- Tjy boe Cf ou{ 3118* tvhhf tu ui bu drjm buf di bohf n jhi ui bwf joejsf duf g gf dut po cf f urh ezobn jdt ui spvhi jouf sbdujpot x ju gvohbmtboe n juf bttpdjbuf t/ Gvsui f sn psf - ui f dpn n po pddvssf odf pgtuspoh boe pcrjhbuf jouf sbdujpot jo f svq. ujwf qf tutztuf n t) Mjoju2: 99- N psbo boe Uf rboh 2: : 9- Trjnqqf st f u brh 3114* tvhhf tut ui bu ui jt n jhi u cf b hf of sbmqi f opn f opo/

Bnd pvhi n boz tqf djf t i bwf sf tqpoef e joejwjevbm jtujdbma up drjm buf di bohf) Cbrh f ubrh 3113- Qbsn f tbo 3117*- di bohjoh drjm buf i bt ui f dbqbdjuz up bnf s tuspoh jouf sbdujpot- ui f sf cz ejtsvqujoh dpn n vojujf t/ Fybn qrft jodmef b ejwf stf bssbz pg tztuf n t- gspn hsbttrboet) Wpjhi u f u brh 3114* up tvcujebmtztuf n t) PjDpoops 311: * up br vbujd dpn n vojujf t jo qjudi f s qrbout) I pf l n bo 3121*/ Ui f tf sf tvrnt joejdbuf ui bu ui f f ggf dut pg x bsn joh po n boz tqf djf t boe tztuf n t x jmmef qf oe po ui f dpn n vojuz dpouf yujo x i jdi tqf. djf t- jodmejoh qf tut- bsf gpvoe/ Ui f sf gpsf - up voef s. tuboe i px drjm buf di bohf x jmmbggf dut qf djf tÿ ejtusj. cvujpot boe qpqvrbujpo ezobn jdt- f ggf dut pg gbdupst tvdi bt uf n qf sbuvsf n vtucf dpotjef sf e x ju jo joubdu dpn n vojujf t/

Bdl opx rfhehn f out

X f ui bol Frjtbcf ui Bref o-Kjn Evodbo-CbvmN bsjop-Li bj Usbo- boe Di sjtujof Wf oejl pt gps i f rq jo dprfhdujoh boe f y. bn jojoh cf f urht- boe Kpi o Nptf s gps jotusvdujpo jo n juf ubypopn z/ Ti bspo N bsjotpo- N jrjrdb N jmaopwjd- boe Mj{ X jm tpo qspwjef e bttjtubodf jo ui f · fre/ X f bqqsf djbuf ui f i rq pg ui f tubgg boe sf tf bsdi f st bu ui f Ef Tpup boe Cbol i f be ObujpobmGpsf tut boe ui f Cjof wjrnh- MB VTEB Gpsf tuTf swjdf Tpvui f so Sf tf bsdi Tubujpo/ Sf tf bsdi x bt tvqqpsf e cz Ob. ujpobmTdjf odf Gpvoebujpo EFC. 1427633 boe Tpvui f so Sf. tf bsdi Tubujpo- Cjof wjrnh- MB HsbouTST 17. DB. 2244123: . 158/

Sf gf sf odf t Djuf e

Bebn t- B/ T/- boe E/ M/ Tjy/ 3118/ Uf n qpsbmwbsjbujpo jo n zdpqi bhz boe qsf wbrhodf pg gvohj bttpdjbuf e x ju ef. wf rpqn f oubmtubhf t pg Ef oespdupovt qpoef sptbf) Dp. rhpquf sb; Dvsdvrjpojebf */ Fowjspo/ Foupn prh47; 75" 83/

Bzsf t- N/ Q/ 2: : 4/ Qrbou ef gf otf - i f scjwpsz- boe drjm buf di bohf - qq/ 86" : 5/ Jo Q/ N/ L bsf jwb- Kf H/ L johtpnvf s- boe S/ C/ I vf z) f et/*- Cjpujd jouf sbdujpot boe hrpcbmdi bohf - Tjobvf s- Tvoef srboe- N B/

Bzsf t- N/ Q/- boe N/ Kf Mpn cbsef sp/ 3111/ Bttf ttjoh ui f dpotf r vf odf t pgdrjm buf di bohf gps gpsf tui f scjwpsf t boe qbu phf ot/ Tdj/ UpubmFowjspo/ 373; 374" 397/

Cbrh- Kf T/- H/ Kf N btuf st- J/ E/ I pel jotpo- D/ Bx n bdl - U/ N/ Cf {f n f s- W L/ Cspx o- Kf Cvuf si fre- B/ Cvtf - Kf D/ Dpvm tpo- Kf Gbssbs- f u brh 3113/ I f scjwpsz jo hrpcbmdrjm buf di bohf sf tf bsdi ; ejsf duf gf dut pg sjtjoh uf n qf sbuvsf po jotf dui f scjwpsf t/ Hrpc/ Di bohf Cjprh9; 2" 27/

Cbssbt- T/ Kf 2: 81/ Boubhpojtn cf ux f f o Ef oespdupovt gspo. ubrjt boe ui f gvohvt Df sbupdztujt n jops/ Boo/ Foupn prhTpd/ Bn / 74; 2298" 22: 1/

Cbssbt- T/ Kf 2: 84/ Sf evdujpo pgqsphf oz boe ef wf rpqn f oujo ui f tpvui f so qjof cf f urh gprpx joh sf n pwbrpgtzn cjpujd gvohj/ Dbo/ Foupn prh216; 23: 6" 23: : /

Cbssbt- T/ K- boe U/ Qfssz/ 2: 83/ Gvohbmtzn cjpout jo u if qspui psbdjd n zdbohjvn pg Efoespdupovt gspoubrjt) Dp. rhpquf sb; Tdpnzujebf */ [/ Bohf x / Foupn prh82; : 6" 215/

Cbsupo- C/ U/- B/ Q/ Cfdl fsn bo- boe P/ K. Tdi n ju{/ 311: / Drjm buf x bsn joh tusf ohu f ot joejsf dujouf sbdujpot jo bo pre. · f re gppe x f c/ Fdprphz : 1; 3457" 3462/

Csjehf t- K. S/ 2: 94/ N zdbohjbmgvohj pg Efoespdupovt gspo. ubrjt) Dprhpquf sb; Tdpnzujebf * boe u if js sf rbujpoti jq up cf f urh qpqvrbujpo usf oet/ Fowjspo/ Foupn prh23; 969" 972/

Csjehf t- K. S/- boe K. D/ N ptf s/ 2: 94/ Sprh pg ux p qi psf ujd n juf t jo usbotn jttjpo pg cmf tubjo gvohvt- Dfsbupdztujt n jops/ FdprhFoupn prh9; : " 23/

Dbsep{b- Z/ K- K. D/ N ptf s- L/ E/ Lrfiq{jh- boe L/ G/ Sbggb/ 3119/ N vnjqbsujuf tzn cjptf t bn poh gvohj- n juf t- of n b. upef t- boe u if tqsvdf cf f urh- Efoespdupovt svï qf oojt/ Fowjspo/ Foupn prh48; : 67" : 74/

Dbssprm B/ M- T/ X / Ubznps- K. Sf hojf sf - boe M/ Tbgsbozjl / 3115/ Fggf dut pg drjm buf di bohf po sbohf f yqbotjpo cz u if n pvoubjo qjof cf f urh jo Csjujti Dpnzn cjb- qq/ 334" 343/ Jo U/ M/ Ti psf - K. F/ Csppl t- boe K. F/ Tupof) f et/*- Obuvsbm Sf tpvsdf t Dbobeb- Dbobejbo Gpsf tu Tf swjdf - Qb. dj · d Gpsf tusz Df ousf Jogpsn bujpo Sf qpsu CD. Y. 4: : - Wjd. upsjb- Dbobeb/

Dppl - T/ Q/- boe G/ Q/ I bjo/ 2: 99/ X pvoe sf tqpotf pg rpc. rpnzn boe ti psurhbg qjof bubdl f e boe sf bubdl f e cz Efo. espdupovt gspoubrjt [jn n fsn bo) Dprhpquf sb; Tdpnzujebf * ps ju gvohbmbttpdjbuf - Dfsbupdztujt n jops) I fehf dpdl * I vou/ Dbo/ K. Gps/ Sf t/ 29; 44" 48/

Dpqqf ehf - C/ S/- G/ N / Tuf qi f o- boe H/ X / Gf rnpo/ 2: : 6/ Wbsjbujpo jo gf n brh tpvu f so qjof cf f urh tj{f boe rjqje dpouf ou jo sf rbujpo up gvohbmbttpdjbuf t/ Dbo/ Foupn prh 238; 256" 265/

Dsp{jf s- M/- boe H/ Ex zf s/ 3117/ Dpn cjojoh qpqvrbujpo. ezobn jd boe f dpqi ztjpnphjdbnn pef rhup qsf ejdudrjm buf . joevdf e jotf du sbohf ti jgu t/ Bn / Obu/ 278; 964" 977/

E brh- WI /- M/ B/ Kpzdf - T/ N dOvnz- S/ Q/ Of jrtpo- N / Q/ Bzsf t- N / E / Grboojhbo- Q/ K. I botpo- M/ D/ Jsrboe- B/ F/ Mvhp- D/ K. Qf uf stpo- f u brh 3112/ Drjm buf di bohf boe gpsf tu ejtuvscbodf t/ CjpTdjf odf 62; 834" 845/

E bwjt- B/ K- M/ T/ K. ol jotpo- K. I / Mbx upo- C/ Ti psspdl t- boe T/ X ppet/ 2: : 9/ N bl joh n jtubl f t x i f o qsf ejdujoh ti jgu t jo tqf djf t sbohf jo sf tqpotf up hrpcbmx bsn joh/ Obuvsf 4: 2; 894" 897/

Fbtuf srjoh- X / F/- Q/ L / Bhhbsx bmQ/ Cbujn b- L / N / Csboef s- M/ Fseb- T/ N / I px ef o- B/ Ljsjrhol p- K. N psupo- K. G/ Tpvttbob- K. Tdi n jei vcf s- f u brh 3118/ Gppe- · csf boe gpsf tu qspevdut- qq/ 384" 424/ Jo N / M/ Qbssz- P/ G/ Dbo. {jboj- K. Q/ Qbnvjl pg- Q/ K. wbo ef sMjoef o- boe D/ F/ I botpo) f et/*- Drjm buf Di bohf 3118; Jn qbdut- Bebqubujpo boe Wvnf sbcjrjuz/ Dpousjcvujpo pg X psl joh Hspvq JJ up u if Gpvsu Bttf ttn f ou Sf qpsu pg u if Jouf shpwf son f oubm Qbof rnpo Drjm buf Di bohf - Dbn csjehf Vojwf stjuz Qsf tt- Dbn csjehf - Vojuf e Ljohepn /

Gsjf ef ocf sh- O/ B/- K. B/ Qpx f rnn boe N / Q/ Bzsf t/ 3118/ Tzodi spozjt epvcrh f ehf ; usbotjf ou ezobn jdt boe u if Bnhf f ggf dujo tubhf tusvdusf e qpqvrbujpot/ Fdprh Mf uu/ 21; 675" 684/

Gsjf ef ocf sh- O/ B/- T/ Tbsl bs- O/ L pvdi pvl pt- S/ G/ Cjnrjoht- boe N / Q/ Bzsf t/ 3119/ Uf n qf sbuvsf f yusf n f t- ef ot juz ef qf oef odf - boe tpvu f so qjof cf f urh) Dprhpquf sb; Dvs. dvrjpojebf * qpqvrbujpo ezobn jdt jo f btu Uf ybt/ Fowjspo/ Foupn prh48; 761" 76: /

Hbhof - K. B/- S/ O/ Dpvrtpo- K. M/ Gpnz{- U/ M/ X bhof s- boe M/ K. Fetpo/ 2: 91/ Bubdl boe tvswjwbnrpg Efoespdupovt gspo. ubrjt jo sf rbujpo up x f bu if s evsjoh 4 zf bst jo Fbtu Uf ybt VTB/ Fowjspo/ Foupn prh: ; 333" 33: /

Hbo- K. 3115/ Sjtl boe ebn bhf pgtpvu f so qjof cf f urh pvu csf bl t voef s hrpcbmrdrjm buf di bohf / Gps/ Fdprh N bobh/ 2: 2; 72" 82/

Hprai bn n fs- E / T/- G/ N / Tuf qi f o- boe U/ E / Qbjof / 2: : 1/ Ui f fggf du pg u if gvohj Dfsbupdztujt n jops) I fehf dpdl * I vou- Dfsbupdztujt n jops) I fehf dpdl * I vouwbs/ cbssbtjj Ubznps- boe TKC 233 po sf qspevdujpo pgu f tpvu f so qjof cf f urh- Efoespdupovt gspoubrjt [jn n fsn bo) Dprhpquf sb; Tdpnzujebf */ Dbo/ Foupn prh233; 518" 529/

I pehf t- K. E/- X / X / Frbn -X / G/ X butpo- boe U/ F/ Of cf l f s/ 2: 8: / Prhpsf tjo di bsbduf sjtujdt boe tvtdf qujcjrjuz pggpvs tpvu f so qjof t up tpvu f so qjof cf f urh) Dprhpquf sb; Tdp. nzujebf * bubdl t/ Dbo/ Foupn prh222; 99: " 9: 7/

I pf l n bo- E / 3121/ Uvsojoh vq u if i fbu uf n qf sbuvsf jo. , vf odf t u if sf rbujwf jn qpsubodf pg upq.epx o boe cpu upn .vq f ggf dut/ Fdprphz : 2; 392: " 3936/

I pgtf uf s- S/ X / - K. C/ N bi gpv{ - L/ E/ Lrfiq{jh- boe N / Q/ Bzsf t/ 3116/ Fggf dut pg usf f qi zupdi f n jtusz po u if jo. uf sbdujpot bn poh f oepqi rpf ejdg vohj bttpdjbuf e x ju u if tpvu f so qjof cf f urh/ K. Di f n / Fdprh42; 64: " 671/

I pgtf uf s- S/ X / - K. Dspojo- L/ E/ Lrfiq{jh- K. D/ N ptf s- boe N / Q/ Bzsf t/ 3117b/ Boubhpojtn t- n vu brjtn t boe dpn . n f otbrjtn t bggf du pvucsf bl ezobn jdt pg u if tpvu f so qjof cf f urh/ P f dprphjb 258; 78: " 7: 2/

I pgtf uf s- S/ X / - L/ E/ Lrfiq{jh- K. D/ N ptf s- boe N / Q/ Bzsf t/ 3117c/ Tf btpobmrezobn jdt pg n juf t boe gvohj boe u if js jouf sbdujpo x ju u if tpvu f so qjof cf f urh/ Fowjspo/ Fo. upn prh46; 33" 41/

I pgtf uf s- S/ X / - U/ E / E f n qtf z- L/ E/ Lrfiq{jh- boe N / Q/ Bzsf t/ 3118/ Uf n qf sbuvsf . ef qf oef ou f ggf dut po n vu. brjtujd- boubhpojtujd- boe dpn n f otbrjtujd jouf sbdujpot bn poh jotf dut- gvohj boe n juf t/ Dpn n / Fdprh9; 58" 67/

Lrfiq{jh- L/ E/ - boe S/ U/ X jrhjot/ 2: : 8/ Dpn qf ujujwf jouf s. bdujpot bn poh tzn cjpujd gvohj pgu f tpvu f so qjof cf f. urh/ BqqrhFowjspo/ N jdspcjprh74; 732" 738/

Lrfiq{jh- L/ E/- K. D/ N ptf s- G/ K. Mpn cbsef sp- S/ X / I pg tf uf s- boe N / Q/ Bzsf t/ 3112/ Tzn cjptjt boe dpn qf uj. ujpo; dpn qrfiy jouf sbdujpot bn poh cf f urfit- gvohj- boe n juf t/ Tzn cjptjt 41; 94" : 7/

Lrfiq{jh- L/ E/- E/ K. Spcjtpo- G/ Gpx rhs- Q/ S/ N jodi jo- G/ Q/ I bjo- boe I / M/ Brrfho/ 3116/ Fggf dut pgn btt jopdvrbujpo po joevdf e prhpsf tjo sf tqpotf jo jouf otjwf rn n bobhf e rpcrpnn qjof / Usf f Qi ztjprh36; 792" 799/

Mbohps- E/ X /- K. S/ Tqf odf - boe H/ S/ Qpi rh 2: : 1/ I ptu fggf dut po gf sujrjuz boe sf qspevdujwf tvddf tt pg Efoespd upovt qpoef sptbf I pql jot) Dprhpquf sb; Tdpnzujebf */ Fwp. nujpo 55; 71: " 729/

Mbti pn c- K. I /- boe U/ F/ Of cf l f s/ 2: 8: / Jowf tujhbujpot pg f hh ojdi f t- f hht- boe sbuf pgpwjqptjujpo gps Efoespdupovt gspoubrjt) Dprhpquf sb; Tdpnzujebf */ Dbo/ Foupn prh 222; 546" 549/

Mjoju- N / K. 2: 99/ Of n bupef . wf dups sf rbujpoti jqt jo u if qjof x jnnejtf btf tztuf n / K. Of n buprh31; 338" 346/

Mpn cbsef sp- N / K- L/ E/ Lrfiq{jh- K. D/ N ptf s- boe N / Q/ Bzsf t/ 3111/ Cjprphz- ef n phsbqi z- boe dpn n vojuz jo. uf sbdujpot pg Ubstpof n vt) Bdbsjob; Ubstpof n jebf * n juf t qi psf ujd po Efoespdupovt gspoubrjt) Dprhpquf sb; Tdpnzu jebf */ Bhsjd/ Gps/ Foupn prh3; 2: 4" 313/

Mpn cbsef sp- N / K- N / Q/ Bzsf t- S/ X / I pgtf uf s- K. D/ N ptf s- boe L/ E/ Lrfiq{jh/ 3114/ Tuspoh ejsf du jouf sbdujpot pg Ubstpof n vt n juf t) Bdbsjob; Ubstpof n jebf * boe Efoespd upovt gspoubrjt) Dprhpquf sb; Tdpnzujebf */ Pjl pt 213; 354" 363/

N psbo- O/ B/- boe B/ Uf rboh/ 2: : 9/ Cbduf sjpdzuf . bttpdjbuf e tzn cjpout pgjotf dut/ CjpTdjf odf 59; 3: 6" 415/

N ptf s- K. D/ 2: 86/ N juf qsf ebupst pgu f tpvu f so qjof cf f. urh/ Boo/ Foupn prh Tpd/ Bn / 79; 2224" 2227/

Nptfs- K D/- boe M/ N/ Spupo/ 2: 82/ Njuft bttpdjbuf e xju tpvu fso qjof cbsl cffuht jo Bmho Qbsjti - MB/ Dbo/ Foupn pm214; 2886" 28: 9/

Qbjof - U/ E/- L/ G/ Sbgg- boe U/ D/ I bssjohupo/ 2: : 8/ Jbuf s bdujpot bn poh tdpmzuje cbsl cffuht- uifjs bttpdjbuf e gvohj- boe rjwf dpojgfs i ptut/ Boov/ Sfw Foupn pm 53; 28: " 317/

PiDpoops- N/ J/ 311: / X bsn joh tusf ohui fot bo i fscjwpsf. qrboujouf sbdujpo/ Fdprphz : 1; 499" 4: 9/

Obi svoh- I / G/- H/ S/ Bmho- boe W T/ Qbufm 3115/ Ebz. ef hsff efwfmpqn fouboe qi f opmphz n pef rjoh pgui f jn. n buvsf tubhf t pgDi sztpqi u bsub bhsjdprb) Di bqvjt*) Dp. rhpquf sb; Di sztpn f rjebf *- bqf tupgf vdbmzquqrbobujpot/ Bvtu/ K Foupn pm54; 288" 294/

Qbsn ftbo- D/ 3117/ Fdprphjdbmboe fwpmzujpobsz sftqpotft up sf df oudrjn buf di bohf / Boov/ Sfw FdprhFwprhTztu/ 48; 748" 77: /

Qfudi fz- P/ M/- Q/ U/ NdQi fbstpo- U/ N/ Dbtf z- boe Q/ K N psjo/ 2: : : / Fowjspon f oubmx bsn joh bmf st gppe.x f c tusvduvsf boe f dptztuf n gvodujpo/ Obuvsf 513; 7: " 83/

Sjdf - B/ W- N/ O/ Ui psn boo- boe E/ X / Mboh ps/ 3118/ Wjsvmodf pg boe jouf sbdujpot bn poh-n pvoubjo qjof cff. uh bttpdjbuf e cmf.tubjo gvohj po ux p qjof tqf djft boe uifjsi zcsjet jo Bmf sub/ Dbo/ K Cpu/ 96; 427" 434/

Svf mK K- boe N/ Q/ Bzsft/ 2: : : / K otf oj jof r vbmjuz qsf ejdut f gf dut pgf owjspon f oubmwbsjbujpo/ Usf oet FdprhFwprh25; 472" 477/

Tf qqbmb S/- B/ Cvdl - boe Q/ Lbjrb) f et/*/ 311: / Bebqubujpo pgGpsf tut boe Qf pqrh up Drjn buf Di bohf ; B HrpcbmBt. tfttn f ouSf qpsu/ JVGSP X psm Tf sjf t Wpmn f 33/ Jbuf s obujpobmVojpo pgGpsf tu Sf tf bsdi Pshboj{bujpot- I f m tjol j- Gjorboe/

TBT Jotujuvuf / 3113/ KN Q- W stjpo 6 vtf sjt n bovbmTBT Jo. tujuvuf - Dbsz- OD/

Tjy- E/ M/- boe C/ K Cf ou{/ 3118/ Uf n qf sbuvsf ef uf sn joft tzn cjpoubcvoebodf jo b n vmjqbsjuf cbsl cffuh.gvohvt f dptzn cjptjt/ N jdspcjprh Fdprh65; 223" 229/

Tjy- E/ M/- boe L/ E/ Lrhq{jh/ 3115/ Efoespdupovt cbsl cff. uht bt n pef mtztuf n t gpsui f tuvez pgtzn cjptjt/ Tzn cjptjt 48; 318" 343/

Tjy- E/ M/- boe U/ E/ Qbjof / 2: : 9/ Fgf dupgn zdbohjbmgvohj boe i ptuusf f tqf djf t po qshf oz tvswjwbmboe f n f shf odf pg Efoespdupovt qpoefsptbf) Dprhpquf sb; Tdpmzujebf */ Fowjspo/ Foupn pm38; 24: 4" 2512/

Trjqqf st- C/- U/ B/ Dpvujoi p- C/ E/ X johi f m- boe K N/ X johi f m/ 3114/ B sfwjf x pg ui f hf ovt Bn zmptuf sfvn boe jut bttpdjbujpo xju x ppex btqt/ T/ Bgs/ K Tdj/ : : ; 81" 85/

Tpl bmS/ S/- boe G/ K Spi mg 2: : 6/ Cjpn fusz- 4se fe/ X / I / Gsff n bo boe Dpn qboz- Of x Zpsl /

Ui bdi f s- S/ D/- boe M/ T/ Qjdl bse/ 2: 75/ Tf btpobmwbsjbujpot jo bdujwjuz pgui f tpvu f so qjof cff uh jo FbtuUf ybt/ K Fdpo/ Foupn pm68; 951" 953/

Ui bdi f s- S/ D/- K M/ Tf bsdz- K F/ Dptuf s- boe H/ E/ I fsufm 2: 91/ Ui f Tpvu f so Qjof Cff uh- Uf di ojdbmCvmfujo 2742/ V/T/ Ef q/ Bhsjd/ Gpsf tu Tf swjdf - Dpn cjof e Gpsf tu Qf tu Sf tf bsdi boe Efwf rpqn f ouQsphsbn - Qjof wjmf- MB/

Uvsdi jo-Q/-Q/M/Mpsjp-B/ E/ Ubzrps-boe S/ G/ Cjmjoht/ 2: : 2/ X i z ep qpqvrbujpot pg tpvui f so qjof cffuht) Dp. rhpquf sb; Tdpmzujebf * , vduvbuf @Fowjspo/ Foupn pm 31; 512" 51: /

Vohf sfs- N/ K- boe N/ Q/ Bzsft/ 2: : : / Drjn buf boe uif opsui f so ejtusjcvujpo rjn jut pg Efoespdupovt gspoubrjt [jn n f sn bo) Dprhpquf sb; Tdpmzujebf */ K Cjphf phs/ 37; 2244" 2256/

W ztf z- K T/- N/ Q/ Bzsf t- N/ K Mpn cbsef sp-S/ X / I pguf uf s- boe L/ E/ Lrhq{jh/ 3114/ Sf mbujwf tvjubcjrjuz pgVjshjojb qjof boe mcrpmz qjof bt i ptu tqf djf t gps Efoespdupovt gspoubrjt) Dprhpquf sb; Tdpmzujebf */ Fowjspo/ Foupn pm43; 779" 78: /

Wpjhi u- X /- K Qf sof s- B/ K E bwjt- U/ Fhhf st- K Tdi vn bdi f s- S/ Cbi sn boo- C/ Gbcjbo- X / I fjosjdi - H/ Lpi mfs- E/ Mjdi uf s- f ubm 3114/ Uspqi jd rfwf mbsf ejgf sf oujbm tf o. tjujwf up drjn buf / Fdprphz 95; 3555" 3564/

X bhof s- U/ M/- K B/ Hbhof - Q/ K I / Ti bsqf - boe S/ O/ Dpvrtpo/ 2: 95/ B cjpqi ztjdbm pef mpgtpvui f so qjof cff uh- Efo. espdupovt gspoubrjt [jn n f sn boo) Dprhpquf sb; Tdpmzu jebf *- ef wf rpqn f ou/ FdprhN pef m 32; 236" 258/

X bmi f s- H/ S/- F/ Qptu- Q/ Dpowf sz- B/ N f o{f mD/ Qbsn ftbo- U/ K D/ Cf cff - K N/ Gspn f oujo- P/ I pfhi .Hvmecf sh- boe G/ Cbjsmjo/ 3113/ Fdprphjdbmsf tqpotf t up sf df oudrjn buf di bohf / Obuvsf 527; 49: " : 6/

X ppupo- K U/ 2: : 5/ Qvujoh ui f qjf df t uphf ui f s; uf tujoh ui f joef qf oef odf pgjouf sbdujpot bn poh pshbojtn t/ Fdprphz 86; 2655" 2662/

Sfdfjwfe 27 Bvhvtu 3121<bddfquf e 8 Kvof 3122/